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THE BOTANICAL REVIEW

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# SOIL MOISTURE IN RELATION TO PLANT GROWTH

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## SOIL AND ITS PHYSICAL CHARACTERISTICS

Some knowledge of the principles governing the distribution and availability of soil moisture is essential to a proper understanding of plant-water relations. Soil, considered in relation to plant growth, is not a mere mass of "dirt", but a complex system consisting of varying proportions of four principal components: mineral materials, organic matter, water and solutes comprising the soil solution, and air. While the amounts of mineral materials and organic matter vary but little in a given soil, the amount of water fluctuates over a considerable range and the amount of air varies approximately inversely with the water content. Furthermore, the proportions of oxygen and carbon dioxide in the soil atmosphere vary with depth, season and other factors (10). In addition to these four components, soil usually contains numerous living organisms, such as bacteria, fungi, algae, protozoa, insects, earthworms and other small animals. These may directly or indirectly affect plant development, and the burrows of earthworms and other small animals provide passageways which facilitate the downward percolation of water through impermeable soil strata.

The characteristics of a soil depend chiefly on the texture or size of mineral particles, the structure or manner in which these particles are arranged, and the amount of organic matter incorporated with the mineral matter. On the basis of texture, soils are usually classified as gravel, sand, loam or clay. The last three classes are most important with reference to plant growth and will be discussed briefly. More detailed discussions can be found in various soils texts (7, 52, 62, 81).

The least complex soil is a sand, which by definition contains less than 20% of silt and clay and is composed largely of simple rock

particles of comparatively large size. Such a soil forms a relatively simple capillary system with large pores or air spaces which insure good aeration and free movement of gravitational water. Sandy soils are relatively inert, both chemically and physically, quite loose and non-cohesive, and have a very low water-holding capacity.

Clay soils are at the other extreme with reference to size of particles, consisting of 30% or more of clay particles, most of them of colloidal or near colloidal dimensions. These particles are usually aggregated together in complex granules which swell and become sticky when wetted. Because of the large proportion of particles of colloidal size in clay, water and minerals are held in much larger quantities and in a more complex manner than in sand. Most soils owe many of their chemical and physical properties to the clay fraction which they contain. The clay particles, because they are flat and plate-like, possess not only the maximum external surface, but also very high cohesive forces. They are usually negatively charged and carry a shell of cations and associated water molecules. The surface possessed by even a small volume of such particles is tremendous. A cubical sand grain one millimeter on the edge has a surface of only six square millimeters, but if divided into cubes of colloidal size, 0.1 micron on the edge, the total surface resulting would be 60,000 square millimeters. Because of their plate-like shape clay particles have even greater surfaces than cubes or spheres of similar volume. Their extensive surfaces enable clay soils to hold much more water than sandy soils, but since the pores are much smaller gravitational water drains off more slowly and they are sometimes poorly aerated.

Loam soils contain more or less equal proportions of clay and sand and therefore have properties which are intermediate between those of clay and sand. They are most favorable for plant growth because they hold more available water than sand, and are better aerated and easier to work than clay.

Soil structure, or the arrangement of soil particles, is important because of its relation to pore size. Soil porosity refers to the portion of the soil volume not occupied by solid particles, but by air and water. It usually amounts to about half of the volume, generally comprising somewhat less than 50% of the total volume in sand and somewhat more than 50% in clay, though exceptions to this exist (94). The total pore space is not so important as the

size of the pores. That portion of the pore space composed of large pores from which water usually drains by gravity and which is therefore normally filled with air is termed the non-capillary porosity to distinguish it from that part of the pore space which is normally filled with capillary water. The large pores and large non-capillary porosity of sandy soils result in better drainage and aeration, but also result in a lower water-holding capacity than in clay soils which have a large proportion of smaller capillary pores. An ideal soil is said to be one which has the pore space about equally divided between large and small or non-capillary and capillary pores (7). Such a soil has enough large pores to permit adequate drainage and aeration and enough small pores to give adequate water-holding capacity. In clay, treatments tending to promote granulation produce larger pores, resulting in a more favorable medium for root growth. The dense mat of roots produced by grass sod seems to promote granulation and good soil structure, while cultivation generally produces the opposite effect (7, 11). The direct effects of root penetration through the soil, followed by their death and decay, is to open up numerous channels and thus to materially increase soil porosity and penetration by air and water. Earthworm activity probably has similar effects.

Soil structure is also affected by the kinds of cations present. According to a summary prepared by Veihmeyer (95), there is evidence from laboratory experiments that various properties, including moisture equivalent, permeability, hardness of crumbs and cohesiveness, are increased by substitution of sodium or potassium ions in the exchange complex and decreased by substitution of calcium or hydrogen ions. Most investigators seem to think these results also apply to field conditions, though few data are available from field tests. Eaton and Horton (30) reported that the wilting coefficient and moisture equivalent of soils partially saturated with sodium were higher than those of the same soils treated with calcium, if most of the soluble electrolytes was first removed. They state that it has been frequently observed that permeability of soil is reduced by irrigation of land with water containing a higher proportion of sodium than of other bases. This is important in semi-arid regions where rainfall is too light to remove the salts concentrated in the surface layer by evaporation of irrigation water.

Appreciation of the importance of soil structure has raised questions concerning the propriety of determining such soil properties

as water-holding capacity, moisture equivalent and permanent wilting percentage on disturbed soil, as is usually done. Soil samples are usually dried, pulverized and passed through a sieve, thoroughly destroying the original structure, before they are subjected to various tests. In recent years a number of methods have been described for obtaining soil samples without disturbing their structure. One type of sampler (21) provides undisturbed soil masses for volume weight and water-holding capacity determinations and for permanent wilting percentage determinations.

The organic matter or humus in soil represents that portion of plant remains, chiefly lignified material, which is most resistant to decay. It resembles clay in some respects, being colloidal with negatively charged micelles surrounded by shells of cations, and shows even more chemical and physical activity than does clay. Because of its very great surface it holds much water, and addition of organic matter to sandy soils increases their water-holding capacity. Its addition to clay may improve the latter's structure and workability, but usually has much less effect on available water content than is commonly supposed because the water-holding capacity of clay is already comparatively high and the unavailable water content of organic matter is very high. A mixture of one-half clay and one-half peat moss by volume held only about 25% more available water than pure clay, while a mixture of one-half quartz sand and one-half peat moss held about 800% more water than pure sand (34). Apparently it is difficult to make any important changes in the available water content of soils under field conditions. In California (96) it was found that addition of as much as 200 tons per acre of manure did not appreciably increase the content of water available to plants in sand, loam or clay soils. In New York (40) additions of 8 and 16 tons per acre of manure for 27 years did not significantly increase the available water-holding capacity of Chenango loam, but did significantly increase the available water-holding capacity of Chenango fine sandy loam.

## SOIL MOISTURE CLASSIFICATION

The classification of soil moisture most familiar to plant scientists is the simple system of Briggs (12) with the addition of water vapor as suggested by Lebedeff (57). This system divides soil moisture into four classes:

*a*) gravitational water, which occupies the larger pores of the soil and drains away under the influence of gravity; it is often injurious to plants if drainage is too slow;

*b*) capillary water, which is held by surface forces as films around the particles, in angles between them and in capillary pores; capillary water moves slowly in the form of liquid from thicker to thinner films, and is the only important source of water for most plants;

*c*) hygroscopic water, which is held on the particles by surface forces and moves in the form of vapor; the moisture remaining in air-dry soil is usually regarded as hygroscopic water and is generally unavailable to plants;

*d*) water vapor, which occurs in the soil atmosphere and moves along vapor pressure gradients; it is probably not used directly by plants.

Such a classification must be regarded as somewhat arbitrary in the light of present-day theories of soil moisture because there really is no sharp boundary between these different classes of soil moisture (97). Under certain conditions capillary water may become gravitational water and hygroscopic water may merge into capillary water. This classification seems sufficiently useful, however, especially to plant scientists, to retain it in spite of its arbitrary nature. A brief discussion of the various types of water follows.

*Gravitational water.* For a short time following a heavy rain or irrigation the soil may be completely saturated with water, the air in it having been displaced from the non-capillary pore spaces between the particles. Under the influence of gravity most of this free water soon percolates downward through the soil toward the water table, unless prevented by some barrier such as a hardpan layer. Within two or three days after a rain all the gravitational water usually drains out of at least the upper horizons of the soil, and the pore spaces become refilled with air. If the soil remains saturated with gravitational water for several days serious injury to root systems may result from lack of oxygen and accumulation of excess carbon dioxide. Obviously gravitational water is therefore of little direct value to most plants and even may be detrimental.

*Capillary water.* After the gravitational water has drained away a soil is said to be at its "field capacity". The water remaining

exists as films around the particles, in the angles between the particles, and in the smaller capillary pores. Much of this water is held rather loosely and is readily available to plants. Some of it, often termed "inner capillary water", is held by the colloidal material and in the smallest pores and is relatively unavailable to plants. As previously stated, the finer the texture of the soil the more surface is exposed and the more capillary water it will hold. Since capillary water moves slowly it is relatively unavailable unless the roots actually come into contact with it. Puri (74) claims that the lower limit of water available to plants is determined principally by the number of pores too small to be penetrated by root hairs. In general, movement of capillary water from moist to dry soil is quite slow, and the significance of this with respect to absorption will be discussed later.

*Hygroscopic water.* The water remaining in a soil in equilibrium with a partly saturated atmosphere is usually termed "hygroscopic water". It is held in a very thin film perhaps 15 to 20 molecules in thickness. The upper limit of hygroscopic moisture is generally supposed to be the moisture content of soil in equilibrium with saturated air, but soil kept in contact with moist air over a long period may accumulate so much water that it actually becomes saturated (52). This illustrates the difficulty of sharply distinguishing between these two classes of soil moisture. Hygroscopic water, if the term is used to refer to the water in approximately air-dry soil, is obviously unavailable to plants.

## SOIL MOISTURE TERMINOLOGY

The literature dealing with soil moisture contains numerous special terms. Many are of interest only to soils men or engineers, but a number of them are frequently used in discussions of plant and soil moisture relations. Among the terms frequently encountered in discussions of plant and soil water relations are "capillary potential, pF value, capillary capacity, maximum water-holding capacity, field capacity, hygroscopic coefficient, wilting coefficient, wilting point, permanent wilting percentage, wilting range, moisture equivalent, readily available water, relative wetness, water-supplying power".

The "capillary potential" or "pressure potential" of a soil, often designated by the Greek letter psi ($\psi$), is a measure of the attractive

forces with which water is held by the soil, or an expression of the work done in moving water against the capillary forces of the soil. Buckingham (17), who originally proposed the term, expressed it as the height in centimeters of a water column which would exert sufficient pressure to move water in a soil at a given moisture content. It may also be expressed in gram centimeters per gram or ergs per gram. The potential of free water, which is the base or reference value from which the potential of soil moisture is measured, is regarded as zero. Since the potential of water in unsaturated soil is lower than that of free water, the potential of soil water must be regarded as having a negative value. The capillary potential increases negatively with decreasing moisture because more energy is required to move water in dry soil than in moist soil. Since it is negative the potential is sometimes expressed as a tension in terms of the height of the water column required to produce it, as for example 250 or 500 centimeters of water, or the corresponding height of a mercury column.

Recently use of the thermodynamic function of "free energy" has been proposed to deal with soil moisture problems (31, 32, 83). It is a more generalized quantity which includes the capillary potential as a special case. The latter deals only with the energy relations resulting from the tension or pressure existing in soil moisture, and excludes the effects of dissolved salts and the possible adsorption of water molecules around soil particles. These are included by the quantity "free energy". The capillary potential is approximately equal to the free energy value when the concentration of solutes is negligible. The free energy and the capillary potential can be measured or calculated from measurements made in various ways, such as by determining the vapor pressure or the freezing point, and by use of the centrifuge, dilatometer, osmotic membranes, tensiometers and pressure devices. Tensiometers (77) are essentially porous clay cups, similar to autoirrigators, connected to a mercury manometer or vacuum gauge which indicates the negative pressure or tension when the water in the cup is in equilibrium with the soil moisture. The capillary potential at various moisture contents is sometimes measured in the laboratory by placing the soil in contact with a porous plate attached to a vacuum line. The soil is subjected to any desired suction and the moisture content is then determined. Unfortunately these methods operate only to

a potential equal to one atmosphere or less, so the higher potentials existing in drier soils are usually calculated from their vapor pressures. Richards (76) has recently developed a method of applying pressure which gives potentials under pressures up to 16 atmospheres or more.

The energy concept of soil moisture is becoming more popular because it indicates the condition of the soil moisture independently of texture, structure or composition. The moisture relations of very diverse soils can therefore logically be compared because, for example, the capillary potential, pF, or free energy of the soil water at the permanent wilting point is approximately the same in all soils.

"Soil pF". Schofield (85) proposed the use of the logarithm of the capillary potential expressed in centimeters of water. He termed this the pF scale by analogy with the pH scale, "p" referring to its logarithmic character and "F" indicating that it refers to the logarithm of the free energy difference. The chief advantage of this scale is that it permits the entire range of soil moisture tension to be shown on one compact scale, although the equivalent water column is almost 10 kilometers (1,000,000 cm.) at equilibrium with 50% relative humidity (pF 6) and about ten times greater at oven-dryness (pF 7). The moisture equivalent is at a pF of about 2.7, the wilting percentage at about 4.2. Water may be regarded as moving along a pF gradient from regions of low pF to regions of higher pF. The pF can be directly determined down to about pF 3 by applying suction to a thin layer of soil, and values for drier soils have been calculated from vapor pressure and freezing point depression data or more recently by application of direct pressures up to 16 atmospheres (76).

The "hygroscopic coefficient" is the moisture content of the soil in equilibrium with an atmosphere of known relative humidity—usually a nearly saturated atmosphere. According to Keen (52) and others, the experimental difficulties inherent in making such determinations render them of very doubtful value, although at relative humidities below saturation reproducible results can be obtained. This value generally is of minor interest to plant scientists.

The "maximum water-holding capacity" is the water held by a thin layer of saturated soil. The soil is placed in a shallow metal container with perforated bottom and allowed to stand in water until saturated. This gives measures of pore space, specific gravity

and expansion on wetting, and Keen (52) recommends it as a measurement useful to the soil scientist. The method of draining surplus water will affect the results obtained, and the results may also vary depending on whether the measurement is made on pulverized soil or a soil mass with undisturbed structure.

The "maximum capillary capacity" of a soil is the maximum moisture content held against gravity and is therefore essentially similar to the field capacity.

The "field capacity" of a soil is the moisture content after the gravitational water has drained away (101), and it is therefore essentially equal to the capillary capacity. Most soils are at their field capacity within two or three days after a rain or irrigation (103). Soil samples in short columns allowed to drain over sand probably reach approximately their field capacity within a few hours. This is not a true equilibrium value, but only a condition of such slow water movement that the moisture content does not change appreciably between applications of water. While most soils reach their field capacity very quickly, the presence of a water table near the surface will greatly prolong the time required for drainage, and if the soil is saturated to a depth of many feet, drainage of the surface layer to field capacity will be much slower than if only the top few feet are wetted. A fine-textured soil overlying a coarse-textured soil will also have a higher field capacity than a uniformly fine-textured soil (103).

The term "moisture equivalent" was introduced by Briggs and McLane (13) to denote the water content of soil which has been subjected to a centrifugal force of one thousand times gravity in a soil centrifuge. The precautions necessary to insure accurate results have been discussed (*e.g.*, 105). The moisture equivalent has been found to be closely related to the field capacity of fine-textured soils but not of sands (101). Work and Lewis (108) found that the moisture equivalent of certain Oregon soils was not equal to the field capacity, and such a relation should not be assumed without actual determinations. The ratio of field capacity to moisture equivalent of certain West Virginia soils is unity in the vicinity of a moisture equivalent of 21% more than unity for soils with moisture equivalents below 21% and less than unity for those with moisture equivalents above 21% (16). Although the equipment is expensive, determinations are so easily made that the moisture equivalent is one of the most frequently determined soil constants.

"Permanent wilting percentage". The moisture content of the soil at the time when the leaves of plants growing in that soil first become permanently wilted has been variously designated as the "wilting point", "wilting coefficient", "wilting percentage", and "permanent wilting percentage". It will be designated as the "permanent wilting percentage" in this paper. Briggs and Shantz (14) first emphasized the importance of this soil moisture content with respect to plant growth and termed it the "wilting coefficient". Their procedure was to grow seedlings in glass tumblers of soil sealed with a mixture of paraffin and vaseline. When the leaves wilted and did not recover over night in a moist chamber the moisture content of the soil was determined by oven-drying a sample at 105° C. and calculating the moisture content as a percentage of the dry weight. Briggs and Shantz stated that this marked the lower limit of soil moisture available for growth, but not the lower limit of soil moisture available for the plants. Although absorption is too slow for growth at moisture contents below the wilting point, plants are able to absorb water from the soil until it is approximately air-dry or until they have died of desiccation. Permanent wilting, according to Briggs and Shantz, does not mark any definite limit in the movement of water from soil to plant, but simply marks the moisture content at which absorption becomes too slow to replace the water lost by transpiration, resulting in wilting. Shull (91) came to similar conclusions regarding the cause of wilting, and these views have been substantiated by more recent investigations and are generally accepted at the present time.

The moisture content of the soil at the time of permanent wilting might conceivably be affected by the species and condition of the plants used in its determination and by the environmental conditions under which it is determined, as well as by the soil texture. Briggs and Shantz (14) concluded, however, that soil texture is the only factor materially affecting the moisture content at permanent wilting. Age of their plants did not materially affect the values, as the same results were obtained with seedlings and well grown grass plants. Plants grown with different amounts of soil moisture wilted at the same moisture content, indicating that drought resistance had not been increased by growing the plants in dry soil. Contrary to previously accepted views, they found no important differences between different species of plants in regard to their ability to reduce

the moisture content of the soil before wilting. The differences observed between various species of crop plants were too small to explain differences in drought resistance, and even these small differences were believed to result from differences in root distribution rather than from differences in forces bringing about water absorption. Similar results have been obtained with a number of crop plants (20). The results and conclusions of Briggs and Shantz have been criticized for various reasons (15, 19, 24, 72, 90), but they are substantiated by more recent investigations. Briggs and Shantz found that while all species wilted at approximately the same moisture content in a given soil there were considerable differences between species in ability to survive in soil below the wilting point. Some species died soon after wilting, while others survived for long periods in a partially wilted condition. Some of the criticisms of Briggs and Shantz' work probably result from failure to differentiate between the early stage of wilting used by them as an end point and later stages approaching the ultimate wilting point of Taylor, Blaney and McLaughlin (92) and Furr and Reeve (37).

The type of plant used in determining the wilting percentage does have some bearing on the reliability of the results. The first requirement is a well-developed fibrous root system which so completely permeates the soil that the moisture content is evenly reduced throughout the soil mass. The leaves must be of a type which show wilting clearly, and plants with heavily cutinized leaves, such as pine needles, are therefore unsatisfactory. The writer found that the wilting point of a sandy loam determined simultaneously with sunflower, black locust and pine seedlings appeared to be highest with sunflower, and lowest with pine seedlings. This probably does not represent any difference between these species in ability to reduce the moisture content, but resulted from the greater difficulty in determining when the pine seedlings had begun to wilt. Moinat (68) suggested that determination of the wilting point may be in error because of the leaves removing water from the stem or other parts of the plant after the soil is really at the wilting point. This would be a negligible factor when oats or other grasses are used as indicators. It probably is also a minor factor if the wilting process is terminated when the first pair or two of leaves have wilted.

A lively controversy arose concerning the influence of atmospheric factors on determination of the wilting percentage. Briggs and Shantz (14) made most of their determinations in a greenhouse where transpiration was very moderate but considered that the values were not materially affected by atmospheric conditions such as humidity or by moderate changes in light intensity. Two other investigators (15, 19) found that plants growing in the open wilted at a higher soil moisture content than plants growing in shade with a lower rate of transpiration. One of these (19) concluded that "for a series of plants grown in any one soil and wilted under a number of aerial conditions, as many different soil-moisture contents are obtained as there are sets of conditions". In another experiment (90) in which several species were wilted under various degrees of shading, it was found that the moisture content of the soil at permanent wilting was lowest in the shade and highest in full sun. Veihmeyer and Hendrickson (102) found the wilting percentage of a particular soil to be remarkably constant, regardless of size of container, species of plant, season of the year, or degree of exposure. Sunflower plants were wilted in the spring and during the hot dry weather of late summer. Some seedlings were allowed to wilt in a moist chamber in a greenhouse, others in a whitewashed greenhouse and still others in the open. The average wilting percentage was the same in all instances, although the rate of evaporation was several times as high when some plants wilted as when others wilted. Furr and Reeve (37) obtained similar results. Discrepancies between the conclusions of various investigators may have been caused in part by differences in opinion as to what constitutes the onset of permanent wilting.

Sachs (84) seems to have been the first to study the effect of soil texture on the availability of water to plants. He found that when tobacco wilted in sand, loam and a mixture of humus and sand, the moisture contents at the time of wilting were 1.5%, 8.0% and 12.3%, respectively. Apparently little attention was paid to this situation until publication of the very extensive work of Briggs and Shantz (14). They found the moisture content at permanent wilting to vary from 1% in sand to 25% in clay and even higher in soils containing much organic matter.

In addition to actually determining the wilting point, Briggs and Shantz attempted to calculate it from the moisture equivalent. They found that for their soils,

$$\text{Wilting coefficient} = \frac{\text{moisture equivalent}}{1.84 \pm 0.013}.$$

This value has frequently been used, but subsequent work by several investigators show that such a relation does not always exist. In an investigation of 60 California soils (101) the ratio was found to range from 1.4 to 3.8. The ratio of moisture equivalent to wilting percentage in three soils on the Duke Forest ranged from 1.57 to 5.65, varying with soil type and horizon (29). Briggs and Shantz also attempted to relate the wilting coefficient to the hygroscopic coefficient, the moisture-holding capacity and the mechanical analysis. The usefulness of any such cross-relating of values is obviously very doubtful, since the relations are not the same in all soils. The moisture content at permanent wilting appears, however, to be logically and consistently related to certain other values. The permanent wilting percentage of most or possibly all soils falls at about pF 4.2 and at the moisture content existing after application of a pressure of 15 atmospheres. The moisture content of a soil at permanent wilting can be determined most reliably by direct observation. Since the term "wilting coefficient" has often been applied to indirect determinations, it would seem preferable to use the term "permanent wilting percentage" to indicate determinations made by the direct method (100).

Wilting, of course, does not begin at a specific moisture content, but it does begin within a very narrow range of soil moisture for which the value given as the permanent wilting percentage is the average. The more care taken in making the determinations, especially in bringing all plants to the same stage of wilting, the more consistent the results. Since the permanent wilting percentage is so stable for a given soil and since it accurately indicates the lower limit of soil moisture available for plant growth, it is perhaps the most important of all soil constants for the plant scientist. Detailed descriptions of the methods used in precise research have been given by several experimenters (14, 37, 108). The writer has obtained satisfactory results with less elaborate methods, merely growing oat or sunflower seedlings in heavily paraffined pint ice cream containers until they are three or four inches high, sealing the soil surface with paraffin and allowing the containers to stand on a partly shaded greenhouse bench until the lower leaves remain visibly wilted over night.

"Wilting range of a soil" is a term applied to the range of soil moisture from the first permanent wilting of the basal leaves of sunflowers to complete permanent wilting of the entire plant (92). Furr and Taylor (38) and Furr and Reeve (37) have presented data on this range, and Furr and Reeve give detailed instructions for its determination. They use the terms "first permanent wilting point" and "ultimate wilting point" to designate the upper and lower limits of the wilting range and like Briggs and Shantz regard the first permanent wilting point as the lower limit of soil moisture available for growth. The moisture in the wilting range, while unavailable for growth, is available for survival, and the proportion of the total available soil moisture which is within this range is great enough to be of considerable significance in plant water relations. In about 80 soils which were studied (37), a minimum of 11% and a maximum of 30% of the moisture content between the moisture equivalent and the ultimate wilting point was in the wilting range.

The "readily available moisture" in a soil is that which can be used by plants in growth and is therefore the moisture above the permanent wilting percentage. While gravitational water is readily available to plants, it usually drains off too soon to be of much importance. The readily available water is therefore usually considered to be that included in the range from field capacity or moisture equivalent down to the permanent wilting percentage. In sandy soils this range is quite narrow, in clay it is quite wide. The advantages of a wide range of available water in carrying plants through droughts or in obviating the need for frequent irrigation is too obvious to need discussion. The relative availability of water in the upper and lower part of this range will be discussed later. As previously stated, plants can absorb water from soils drier than the permanent wilting percentage, but absorption is too slow for growth.

"Relative wetness" is a term applied to the ratio of moisture content to moisture equivalent (23). Dividing the moisture content by the moisture equivalent enables comparisons to be made between soils or soil horizons which differ in texture. This is particularly useful in following moisture changes at various depths or in various parts of an orchard or field where the soil is not uniform in texture.

The "water-supplying power" of the soil refers to the rate at which water moves from soil to an absorbing surface, such as a

root. This term is generally used to refer to measurements made with the "soil point cones" of Livingston and Koketsu (59*a*).

### MOVEMENT OF SOIL MOISTURE

Movement of soil moisture is relatively complex because of the various directions and states in which it moves and the various forces operating to cause its movement. Downward movement occurs when the soil is being wetted by rain or irrigation, some upward movement occurs when the surface is drying by evaporation, and lateral movement also occurs. Water moves as liquid in capillary films and in the larger or non-capillary pores. Appreciable movement also occurs in the form of vapor along vapor pressure gradients and in convection currents of the soil atmosphere. The forces causing movement of liquid water are chiefly gravity, hydrostatic pressure and capillary forces. Because it is often difficult to determine precisely which forces are bringing about water movement, it is considered best to regard water as moving along gradients of decreasing free energy, a statement that is true regardless of the nature of the forces involved.

*Infiltration.* Infiltration of water into the surface is the first step in wetting a soil, and the rate of infiltration into a given soil is a very important factor in determining how much of a given rainfall will be accumulated in the soil and how much will be lost by run-off. A relatively impermeable surface is developed on a bare soil surface after only a few minutes' exposure to rainfall. This results from the packing of small particles around the larger ones by rain drops and surface flow so that water cannot penetrate freely. Formation of such a layer can be avoided and run-off can be greatly decreased by mulches and incorporation of organic matter into the surface of the soil. According to Duley (28), formation of an impermeable surface layer has more effect on infiltration of water into Nebraska soils than soil type, slope, moisture content or profile. Run-off and accompanying erosion, in his opinion, can be practically eliminated by maintaining a mulch of crop residues on the soil. While infiltration into a bare soil is much more rapid at first if it has been cultivated, the rate decreases very rapidly after the first 15 to 30 minutes, and on both cultivated and uncultivated soils it soon reaches a constant rate which is determined by the rate of downward percolation through the deeper soil horizons.

*Movement of gravitational water.* This movement after the water has penetrated into the soil is chiefly affected by number, size and continuity of the air spaces or non-capillary pores through which it percolates. It usually moves very freely through the large pores of sandy soils, and such soils are generally quickly drained to field capacity. Movement is less rapid through clay because the pores are much smaller; they are frequently blocked by the swelling of colloidal gels, and air is often trapped in them. Lutz (61) found the permeability of clay to decrease as the hydration of the particles increased. Movement of gravitational water is frequently hindered by impermeable subsoil layers which trap air as well as water. Movement is facilitated by worms and other animal activity and by decay of roots, all of which leave passageways. In general, unless a hardpan interferes or the soil is saturated to a shallow water table, gravitational water can be expected to drain out of the surface layer within two or three days after rain or irrigation.

*Movement of capillary water.* The earlier discussions of the movement of soil moisture were based on a relatively simple concept of the soil as an aggregate of capillary tubes of various dimensions, and many present-day discussions make use of this capillary theory. According to this theory, as developed by Briggs (12), soil moisture exists principally as continuous thin films around the soil particles and in the smaller spaces and angles between them. These films are under great inward pressure because of the surface tension of the water, and water therefore tends to move from regions with thicker films to regions with thinner films.

While the foregoing assumptions are correct, the capillary theory has been found inadequate to explain certain observed facts and has therefore been sharply criticized. Dissatisfaction with the inadequacy of the capillary theory led to the gradual development of a theory based on the energy relations or work done during the movement of water. Buckingham (17) suggested that movement of water through the soil might be compared to the movement of heat or electricity through a conductor. He considered the driving force to be the difference in attraction for water between two portions of soil having different moisture contents and proposed the term "capillary potential" for the force required to move a unit mass of water from a unit mass of soil. This theory was further developed by various other workers (7, 32, 39, 52, 75, 83) to whom the

reader is referred for more detailed discussions of various aspects of the theory.

According to certain writers (7, 97), the most important implication of the potential theory of soil moisture is that there are no such sharp boundaries or differences between various types of soil moisture as are indicated by the terms "gravitational", "capillary" and "hygroscopic water". Various methods of measuring the potential or force with which water is held by soil at various moisture contents agree in indicating that the potential is directly related to the moisture content. When the potential is plotted against decreasing soil moisture it forms a smooth curve, indicating that there is no real change in the state of water as the moisture content decreases from the field capacity past the permanent wilting percentage down to an oven-dry condition, but merely an increase in the energy required to move it. The permanent wilting percentage falls in the region of greatest curvature of the curve for potential over soil moisture, while the field capacity falls in the region where it becomes almost flat.

It has been proposed (31, 32) that the thermodynamic concepts of free energy be applied to discussions of water movement in the soil and through the plant. Such a treatment of soil moisture movement is based on sound principles and is very useful to the soil physicist, but unfortunately many plant scientists are not sufficiently familiar with the mathematical methods used to fully understand such a treatment. It is more intelligible to most workers and for most purposes it is just as satisfactory to discuss the movement of moisture in the more familiar terms of gradients of diffusion pressure, vapor pressure or diffusion pressure deficit (66) which are also based on energy relations. The plant scientist is primarily concerned with understanding the factors which affect the availability of water and its movement from soil to plant roots. Movement of soil moisture can be discussed in conventional terms if we remember that regardless of the terminology its movement is determined by differences in energy or in the forces with which it is held in different regions of the soil. Using this conventional terminology, we may say that water flows under the influence of gravity, moves in capillary films and diffuses as vapor, but it always moves along a gradient of decreasing free energy. Its energy is highest in free water, lower in moist soil and still lower

in dry soil. Movement of capillary water is materially affected by soil texture, being most rapid in sandy soils and slowest in clay soils at saturation, but in drier soils the effects of texture are reversed, movement being slowest in sands and most rapid in clay (70). Height of capillary rise also depends on texture, being greatest in clays and least in sands. In no instance, however, has capillary rise been found to be as great as would be expected from calculations based on size of soil particles. Neither has the movement of capillary water proved to be as rapid as it was once supposed to be. Early discussions of this subject gave the impression that as rapidly as water is removed from the soil particles in contact with the roots it is replaced by capillary movement from more distant soil particles. More recent investigations indicate that capillary movement of soil moisture from moist to drier regions is very slow except where the water table is within three or four feet of the surface. Of course, some movement always occurs from regions with thicker films to regions with thinner films, provided continuity of films exists, but such movement is much more rapid in saturated soil than in dry soil. Moore (70) found very little unsaturated flow of moisture in soils at or below the moisture equivalent. Veihmeyer and Hendrickson (99) placed a mass of soil wet to field capacity in a large cylinder with dry soil on each side of it. After 139 days water had moved only eight inches into the dry soil.

Since capillary movement is so slow in soils drier than field capacity it is probable that during periods of rapid transpiration the available water on soil particles in contact with the roots is removed much faster than it can be replaced by capillary movement. Thus each absorbing root may become surrounded by a slender cylinder of soil from which all available water has been removed, although soil a few millimeters away is still at field capacity. Data of Richards (76), however, indicate that water movement possibly may occur fairly rapidly over distances of a few millimeters. He found that a pressure of 16 atmospheres reduced the moisture content of a soil layer five to ten millimeters in thickness from saturation to below the permanent wilting percentage in 24 to 36 hours. In his experiments he displaced water from a moist soil through a collodion membrane, but did not cause it to move from moist soil into dry soil.

*Movement of water vapor.* As the soil dries out the water films become discontinuous and capillary movement ceases. Any water

movement in air-dry soils must be in the form of vapor. According to Lebedeff (57), in soil above its hygroscopic coefficient the atmosphere is normally saturated. Under field conditions, therefore, the soil atmosphere is always saturated, except the surface layer which occasionally becomes air-dry. Movement of water vapor is along vapor pressure gradients; hence it is affected by the relative temperatures and vapor pressures of various horizons of the soil and of the soil and air. Lebedeff states that the movement of water in the form of vapor is of considerable importance, especially in southern Russia and other semi-arid regions where there is no direct connection between the water table and the capillary water in the upper layer. Film movement is exceedingly slow under such conditions, so the effects of movement of water vapor are more noticeable. Lebedeff found that in winter appreciable quantities of water move from warmer, deeper levels to the cooler surface where it condenses, the amount so moving in one winter amounting to 66 mm. During a cool period in summer or autumn when the surface layer is cooled, water moves from the deeper levels to the surface whence it evaporates during warmer periods, thus slowly drying out the deeper layers. Ordinarily the surface layer of the soil is warmest during summer, and presumably some water vapor then diffuses downward where it condenses in the cooler soil, forming liquid water. According to Lebedeff, this is an important source of ground water in southern Russia. During the night the surface layer becomes cooler than the soil a few centimeters below the surface, while the reverse is ordinarily true during the day. These diurnal variations in soil temperature produce variations in vapor pressure which result in diurnal variations in water movement. Lebedeff calculated that in the vicinity of Odessa over 70 mm. of water are condensed in the surface layer of soil annually during periods when it is cooler than the air above it.

*Evaporation.* The quantity of water lost from soil by evaporation has been the subject of considerable controversy. The amount of water vapor lost depends primarily on the steepness of the vapor pressure gradient from soil to air which in turn depends on both soil and atmospheric factors. The vapor pressure of the atmosphere is affected chiefly by the humidity of the air. Air movement is also important because it changes the air in contact with the soil surface, preventing it from becoming saturated. The principal soil factors

affecting evaporation are temperature and moisture content. Differences in evaporation from dark- and light-colored soils and from north- and south-facing slopes result from differences in temperature.

It is obvious that evaporation from a dry soil surface will be much less than from a moist one because diffusion of water vapor through the soil is very slow. Since when no rainfall occurs the only way the soil surface can be kept moist is by upward capillary movement of water, it has long been assumed that prevention of capillary movement by cultivation will greatly reduce loss by evaporation. Experiments by King (53) showed that less than half as much water was lost from soil covered with a loose dry surface layer two or three inches deep as from an undisturbed surface. King's experiments were with columns of soils in contact with free water. According to Baver (7), Eser had shown in 1884 that evaporation from soil in contact with free water is two to four times as fast as from well drained soils. Unfortunately most people failed to realize that evaporation from soil in contact with a water table occurs much more rapidly than evaporation from soil that does not have a water table near the surface. As a result of this misunderstanding the advantages of a dust mulch in agricultural practice were greatly overemphasized.

More recent experimental work has shown that evaporational losses are less than commonly supposed and that they are not much reduced by cultivation. This is primarily because the water table is so far below the surface in most cultivated land that little upward movement to the surface can occur. Considerable experimental evidence is available which indicates that if the water table is even a few feet below the surface little upward movement of water occurs. Shaw and Smith (89) found considerable water movement to the surface of Yolo sandy loam and Yolo loam with a water table four feet below the surface, but very little when it was ten feet below the surface. They concluded that no appreciable upward movement of water to replace loss by evaporation occurs in these soils when the water table is ten or more feet below the surface. Other investigators have found evidence of slow or negligible capillary rise where the water table is more than a few feet below the surface (18, 52, 80, 96). Where rainfall seldom or never wets the soil to the water table, as in much of the plains area, upward movement is probably

negligible. In such soils removal of water by transpiring plants is a much more important factor in drying out the soil than evaporation (22).

Veihmeyer and Hendrickson (102) cite work in Russia and in this country indicating that little water is lost by evaporation from below the first foot. It has been demonstrated (93) that under California conditions most of the water lost by evaporation comes from the upper four inches, much less from the second four inches and very little from below eight inches. By the time the surface soil has dried sufficiently to permit cultivation considerable moisture has already been lost and more is lost from the freshly stirred soil. In general, most soil appears to dry out to about the same extent and the same depth, whether cultivated or not, unless the water table is within a few feet of the surface. Cultivation may reduce loss by evaporation on soils which crack badly, but it is claimed (103) that the cracks in most California soils, including clays, are too shallow to increase water loss seriously. Cultivation of summer-fallowed land may of course be necessary to prevent a crop of weeds from removing the accumulated moisture. This problem is discussed at length by Lyon and Buckman (62, 223–227).

While dust mulches seem to be ineffective, it appears that mulches of straw, grass, leaves, paper and similar materials are usually much more effective in reducing water loss. This is partly because they shade the soil, reducing its surface temperature, and partly because they lengthen the diffusion gradient from soil to air and protect the soil surface from the drying effects of wind. Russel (82) considers mulches to be effective only in preventing drying of the surface layer because he says a layer of dry soil is a better insulator than the average mulch and also more impervious to water vapor.

The relative amounts of water removed from the soil by evaporation and by transpiration are of interest. It is generally accepted that plant transpiration is the chief means by which water is removed from soils and that transpirational losses far exceed losses by evaporation. If evaporation removes water only from the surface foot of soil the remainder of the soil moisture would remain untouched were it not for the roots of plants. Orchard soils in the East are sometimes dried to the wilting percentage to a depth of two or three feet within three weeks (64), and prune trees exhaust the readily available water in the top six feet of soil in about six

weeks in midsummer at Davis, California (44). It was found (103) that mature peach trees in the Sacramento and San Joaquin valleys of California absorb the readily available water to a depth of six feet from sandy soil in about three weeks and from clay loam soil in about six weeks. Citrus fruits on sandy loam soils four to six feet deep in San Diego County require irrigation every six weeks during summer, and on more shallow soils irrigation is required more frequently. In such instances loss by transpiration is several times greater than loss by evaporation. In certain experiments (96) a tank with bare soil surface lost 18.9 pounds per square foot of surface in four years, equivalent to a depth of 3⅜ inches of water, or less than one inch per year. A four-year-old prune tree growing in a similar tank lost 1,250 pounds of water by transpiration in one growing season. An acre of deciduous fruit at Davis, California, used eight acre-inches of water in about six weeks in mid-summer, or about one pound per square foot of soil surface per day. It seems clear that plant transpiration is the chief means by which capillary water is lost from the soil, and it therefore appears that maintenance of vegetation cover on watersheds decreases the amount of water stored in the soil. This of course does not reflect on the possible importance of vegetation in reducing erosion and consequently preventing silting up of reservoirs. Kittredge (54) stated that a forest transpires more water than would be lost by evaporation from the same area, hence more water could be obtained from a bare watershed than from a forested one. He recognized the need for plant cover to control erosion and slow down run-off and suggested that species with low transpiration rates be selected, recommending scrub oaks and grasses for California.

### AVAILABILITY OF SOIL MOISTURE TO PLANTS

The gravitational water occurring in saturated soils is readily available to plants but is seldom present long enough to contribute much to plant growth. If it does remain more than a day or two its injurious effects overshadow any benefits resulting from its availability. For most plants, then, the water readily available for growth is the capillary water in the range between the field capacity and the permanent wilting percentage. The best moisture supply for growing plants is afforded by soils in which this range of available water is wide. Soils show great variations in this respect, but

sandy soils generally have narrow ranges of available water and clay soils wide ranges. Among some soils used by the writer (56) was a pure sand containing only 2%, a sandy loam containing 14% and a clay containing 19% of readily available water. Occasionally soils with high moisture equivalents and field capacities also have very high wilting percentages and contain but little readily available water. For example, in a California study (104), a clay was found to have a moisture equivalent of 31% and a wilting percentage of 25%; it therefore contained only 6% of available water or less than many sandy soils.

Plants growing in soils with a low storage capacity will exhaust the readily available water and suffer from desiccation much sooner than plants growing in soils with a very large storage capacity. Where irrigation is practiced the more frequent applications required result in much greater waste of water by run-off and evaporation than where a few irrigations suffice. This is especially important with shallow-rooted crops, and Veihmeyer and Hendrickson (104) cite several examples of such occurrences.

Much discussion has occurred as to whether water is equally available over the entire range from field capacity to wilting percentage. Veihmeyer and Hendrickson have repeatedly stated that water either is available or is not available to plants, and that it is equally available over the entire range from field capacity down to the wilting point where it becomes unavailable for growth. They have reported results of experiments indicating that the growth and quality of apples and pears (47), grapes (43), peaches (42), prunes (44), walnuts (45) and cotton (1) were not affected by the moisture content of the soil unless it fell to the wilting percentage and remained there for some days. These plants did no better on frequently irrigated plots than on plots where the soil moisture was allowed to fall to the permanent wilting percentage before water was applied. The seeds of many species are reported to germinate equally well over the entire range of moisture content from wilting percentage to field capacity (27). A few, however, germinated better at 1% or 2% above field capacity, and celery seed was found not to germinate at all in the lower range of soil moisture.

The apparent equal availability of water over the entire range is explained on the basis that there is but a small change in the forces with which water is held by the soil over the range from field

capacity to permanent wilting percentage. The permanent wilting percentage occurs at the moisture content where these forces begin to increase very rapidly, and a small decrease in soil moisture therefore is accompanied by a very rapid increase in the force required to move water from soil to roots.

Considerable evidence is available indicating that water is not equally available to plants over the entire range from field capacity down to permanent wilting. The growth rate of apples in Maryland orchards was reduced when the driest part of the root zone approached the permanent wilting percentage, which was long before the entire root zone was dried to that point (64). Stomatal behavior of apples (64) and peaches (50) was also affected by soil moisture, the stomates being open for a shorter period each day in dry than in moist soil. Premature stomatal closure presumably reduces photosynthesis, resulting in a deficiency of carbohydrates. It was found that in very heavy soils in Oregon the rate of growth of pears is closely related to the moisture content of the upper three feet of soil (2, 58). The fruits suffered reduction in size when the soil moisture dropped below about 70% of the readily available moisture. Trees in these soils have very uneven root distribution, and it may be that while the soil in contact with the roots was at the permanent wilting percentage considerable volumes of soil not penetrated by roots were left at field capacity. As a result the average moisture content would appear to be above the wilting percentage, although the moisture content of the soil in which the roots were growing was actually reduced to the wilting percentage. The transpiration rate of loblolly and shortleaf pine seedlings grown in containers decreased with decreasing moisture content before the permanent wilting percentage of the soil was reached (86). This, likewise, might have resulted from uneven absorption of water because of uneven distribution of root systems. Furr and Taylor (38) found that lemons on shallow soil underlain by dense subsoil suffered sufficient water deficit to cause reduction in size of fruit before the moisture content of all the soil in the top foot was reduced to the permanent wilting percentage. They suggested that some discrepancies in conclusions regarding the availability of water result from differences in judgment as to what constitutes permanent wilting. In a heavy clay soil with a field capacity of 33% the basal pair of leaves of well established sunflower plants wilted at 20.2%,

but the entire plants did not wilt until the soil moisture was lowered to 16.2%.

The growth rate of sunflower plants was affected by small differences in soil moisture content, even though the moisture content was never allowed to fall to the permanent wilting percentage (65). Growth of young maize plants was also slowed by decreasing soil moisture and ceased before the soil moisture content fell to the permanent wilting percentage. Water appeared to be less available for growth from a moisture content 2% or 3% below capillary capacity, and growth ceased while 3% of available water remained in the soil (25). Growth of *Cyperus rotundus* in pots also appeared to be checked by decreasing availability of water in soil which was always above the wilting percentage (26). Each decrease in the minimum soil moisture percentage reached before rewetting to saturation resulted in a significant decrease in weight of the tops of nut grass. Tuber development was decreased significantly by decreased soil moisture from a moisture content only 2% below the moisture equivalent. The growth and yield of kidney beans were reduced if the soil was allowed to dry part way down to the permanent wilting percentage before watering, even though the moisture content never actually reached the permanent wilting percentage (6).

It was found that a decrease in soil moisture from field capacity to the permanent wilting percentage (first permanent wilting of basal leaves) caused the osmotic pressure of sunflower plants in dry air to increase about five atmospheres and that of plants in moist air to increase about two and one-half atmospheres (37). From these and other data the investigators concluded that plants are subjected to progressively increasing water deficit from a moisture content about half way between the moisture equivalent and the permanent wilting percentage down to the permanent wilting percentage. This is in accord with the observation of the writer (56) that exudation from the stumps of detopped plants ceases while about 45% of the soil moisture available to intact plants is still present. This situation probably results from the fact that the roots alone cannot absorb water against a potential of more than one or two atmospheres, but when attached to a transpiring shoot they can absorb against a potential of several atmospheres. Intact plants can therefore absorb water from much drier soil than can isolated root systems.

The contradictory opinions concerning the availability of water held by various investigators results at least partly from differences in the soil types used, differences in opinion as to what constitutes permanent wilting and differences in interpretation of the data. Where the soil is thoroughly and uniformly permeated by roots it is likely that plants can reduce the average moisture content much nearer the permanent wilting percentage without suffering from a water deficit than in heavy soils where root systems are scanty and unevenly distributed. There is no doubt that more energy is required to move water from soil to roots in a dry soil than in a moist soil. This may not immediately decrease transpiration or growth because as the diffusion pressure deficit of the soil increases, the osmotic pressure and diffusion pressure deficit of the plant may at first increase proportionately. Thus the same gradient from soil to root is maintained, while the increased osmotic pressure of the plant sap does not materially reduce transpiration (36). There is, however, an abundance of data indicating that as the soil moisture decreases to the lower half of the range of readily available water, growth and yield are often decreased before the permanent wilting point is reached.

*Concentrataion of soil solution.* Another factor affecting the availability of soil moisture is the concentration of the soil solution. It is recognized that high soil concentration may hinder plant growth by toxic effects of the ions as well as by their osmotic effects, but the latter often seem to be quite important. Addition of NaCl producing an osmotic pressure of four atmospheres caused severe wilting of tomato plants (60). In other experiments high solute concentration increased hydrostatic stress and seriously checked growth of tomatoes (41) and kidney beans (6). It was reported from California (63) that normally fertile irrigated soils had a soil solute concentration at the permanent wilting percentage of 1.3 to 1.8 atmospheres. Some soils with osmotic pressures at the permanent wilting percentage of two to four atmospheres produced good crops of alfalfa, cotton and wheat, but those with higher values showed reduced yields, and soils with values of 40 atmospheres or higher were barren.

*Soil temperature* also affects the availability of water to plants. Many years ago Livingston suggested that temperatures probably markedly influenced the water-supplying power of soils (73). The

writer (55) found that the water-supplying power at 0° C. was only about half as great as at 25° C. The decreased rate of movement from soil to absorbing surface results principally from the increased viscosity of water at low temperatures.

## MEASUREMENT OF SOIL MOISTURE

Since a review of this subject by another author is expected to appear in this journal the measurement of soil moisture will be discussed very briefly. Two types of methods are used, those giving the actual moisture content and those measuring the forces with which moisture is held or the rate at which it is supplied to an absorbing surface. Livingston and his co-workers (73, 107) have frequently stated that the capacity of the soil to supply water to roots is the essential factor of soil moisture as related to plant growth, and all other factors such as texture, water-holding capacity and permanent wilting percentage are important only as they affect the water-supplying capacity of the soil. This view led to the development of soil point cones to measure the water-supplying power of the soil (59*a*).

The actual moisture content of the soil is usually expressed as a percentage of the oven-dry weight, but it could perhaps be expressed more advantageously on a volume basis. The primary interest is in the volume of water available to the roots occupying a given volume of soil, rather than the weight of water in a given weight of soil (7). Various methods have been developed to determine soil moisture without the delay required by oven-drying and without the disturbance caused by sampling. Attempts have been made to determine soil moisture electrically by measuring the electrical conductivity (9), electrical capacity (4, 5), dielectric constant (35) and heat conductivity (48, 88). Physical methods include use of tensiometers (77, 78, 98), porcelain soil point cones (59*a*), and devices to measure the pressure required to penetrate a soil mass (3). Several of these methods can be used to measure moisture content in the root zone without disturbing the roots, a procedure likely to yield much useful information.

## EXPERIMENTAL CONTROL OF SOIL MOISTURE

The older literature dealing with soil moisture as a factor in plant growth frequently described experiments in which plants were said

to have been grown in containers maintained at certain definite moisture contents, as at 10%, 15%, 20% and 25% of the dry weight of the soil. Other papers have mentioned maintenance of soil moisture at optimum, sub-optimum and supra-optimum contents. Engineers have also described methods of wetting soil to be used in construction to some predetermined moisture content by sprinkling a certain amount of water over the surface.

The impossibility of doing these things should have been realized by all who have observed the distribution of moisture in the soil after a rain. Strange to say, however, it was not until comparatively recently that Shantz (87) and Veihmeyer (93) called attention to the fact that if a small quantity of water is applied to a mass of dry soil the upper layer is wetted to the field capacity and the rest of the soil mass is completely unaffected. Addition of more water results in wetting the soil to a greater depth, but there will always be a sharp line of demarcation between the wetted and unwetted soil. This situation has been observed by everyone who has dug in soil following a summer shower and observed the sharp line of demarcation between the wet soil and the dry soil beneath. Since the field capacity is the amount of moisture held against gravity it is obviously impossible to wet any soil mass to a moisture content less than its field capacity. If a container is filled with dry soil having a field capacity of 30% and enough water is added to wet the whole mass to 15%, one half of the soil will be wetted to field capacity and the other half will remain dry. Obviously the earlier investigators did not really maintain their plants at the specified soil moisture contents, but merely gave them various amounts of water distributed in various proportions of the soil mass. The difficulties of controlling soil mosture have recently been discussed (46).

Numerous investigators have attempted to devise means of controlling the moisture supply and improving its distribution in the soil. Livingston (59) developed the use of porous porcelain cups buried in the soil and connected to a reservoir as a means of controlling the supply of moisture, and this system later became known as the auto-irrigation system. He attempted to limit the water supply by introducing mercury columns of various heights between the irrigator cone and the reservoir, thus increasing the tension necessary to bring about water movement from reservoir to soil. Unfortunately there is a tendency for roots to become massed

around the irrigator cones, somewhat nullifying the control, as they absorb directly from the surface of the cones rather than from soil which has come into equilibrium with them. An improvement in moisture distribution is afforded by the use of double-walled pots with a space for water between the glazed outer wall and the porous inner wall (107). The high cost of these containers has prevented their extensive use. Richards and Loomis (79) found double-walled pots maintained a constant soil moisture content for small plants with low tensions (short mercury columns) but not for large plants which removed water rapidly. Even with tensions as low as two to four centimeters of mercury, water was removed faster than it could be supplied. This is because water moves so slowly from wet to dry soil. Numerous tests indicate that many greenhouse plants grow better when supplied with water by some type of auto-irrigator than when watered manually. Use of short pieces of glass rope to supply water to potted plants has recently been described. One end of the rope is pulled through the hole in the bottom of a pot and spread out in contact with the soil mass, while the other end dips into a reservoir. Such devices are particularly useful for house plants which usually are over or under watered. They have also been successfully applied to watering seed flats and greenhouse benches (71).

A number of methods of controlling soil moisture content have been described (8, 33, 49, 67, 69), but none is entirely successful. It seems probable that there is no satisfactory method of constantly or permanently maintaining any soil at a moisture content below its field capacity. Plants growing in the soil may be allowed to reduce the soil moisture to any desired level between field capacity and permanent wilting percentage before applying water, but the moisture content cannot be maintained at any constant level within this range. Most of the proposed control methods simply reduce the amount of water per plant by reducing the soil mass which is wetted, and none of them permanently maintains the entire mass of soil at a uniform moisture content below its field capacity. Discussions of the "optimum" soil moisture content are therefore largely academic and have little relation to actual field conditions. Soil moisture content as related to plant growth can be evaluated only in terms of its relation to the field capacity and the permanent wilting percentage of the soil in which the plants are growing.

SUMMARY

The soil is a complex system consisting of four principal components: mineral materials, organic matter, water and solutes comprising the soil solution, and air. The characteristics of a soil depend chiefly on the texture or size of the mineral particles, ranging in order of decreasing size from sand through loam to clay; on the structure or manner in which these particles are arranged, which determines the number and size of pores; and on the amount of organic matter incorporated with the mineral matter.

Soil moisture is commonly classified as gravitational, capillary and hygroscopic water and as water vapor. Capillary water, which occurs as films around the particles and in angles and the smaller pores between them, usually is the only form of moisture available to plants. There are no definite boundaries between these various types of soil moisture, and they are to be regarded as convenient but wholly artificial categories.

In a soil thoroughly wetted by rain or irrigation the gravitational water usually drains away within one or two days leaving the moisture content at the "field capacity". The field capacity usually approximates the value known as the "moisture equivalent", which is the moisture content of a soil that has been exposed to a centrifugal force of 1000 times gravity. The "permanent wilting percentage" is the moisture content of a soil at which permanent wilting of plants growing therein first becomes apparent, because water no longer moves from soil to roots fast enough to replace the losses by transpiration. That portion of the soil water which is readily available for growth lies between the field capacity and the permanent wilting percentage. The moisture content at the permanent wilting percentage depends on the soil texture, being lowest in sandy soils and highest in clay soils. Obviously the wider the range between the field capacity and the permanent wilting percentage the more water is available for plant growth.

It is sometimes claimed that water is equally available to plants over the entire range from field capacity to permanent wilting percentage, but there is considerable evidence that water becomes progressively less available in the lower part of this range.

Movement of soil water is caused principally by gravity, hydrostatic pressure and capillary forces, the last resulting from differences in curvature and thickness of water films. Since it is often

difficult to distinguish between these forces it is convenient to speak of the movement of water along a gradient of decreasing free energy. The work done in moving water against the attractive forces of the soil increases with decreasing soil moisture. It is often measured in terms of height of an equivalent column of water or mercury and designated as the "capillary potential" or "pressure potential".

Movement of capillary water in a soil mass below the field capacity and lying more than a few feet above a water table is extremely slow. It is therefore likely that relatively little water moves toward the roots and that most soil moisture becomes available only as roots come in contact with it as a result of their elongation through the soil. It has been demonstrated that little or no water is lost by evaporation from below the surface 8 to 12 inches, and dust mulches are therefore relatively ineffective in reducing losses by evaporation.

Soil moisture is usually expressed as a percentage of the oven-dry weight of the soil. It would be more satisfactory if it were expressed as a percentage of its volume, but such determinations are difficult. The moisture content of soil can be measured in place by determinations of electrical conductivity and capacitance, of dielectric constant and of heat conductivity, and indirectly by use of soil point cones and tensiometers.

Numerous attempts have been made to grow plants at various moisture contents between field capacity and permanent wilting percentage. It is impossible to half wet a soil, however, and it appears practically impossible to permanently maintain any intermediate moisture contents. If insufficient water is added to a soil mass to wet it all to the field capacity, a part of it will be wetted to the field capacity and the remainder will remain unaffected.

## LITERATURE CITED

1. Adams, F. *et al.* Cotton irrigation investigations in San Joaquin Valley, California, 1926 to 1935. Cal. Agr. Exp. Sta., Bull. 668. 1942.
2. Aldrich, W. W. and Work, R. A. Evaporating power of the air and top-root ratio in relation to rate of pear fruit enlargement. Proc. Am. Soc. Hort. Sci. **32**: 115–123. 1934.
3. Allyn, R. B. and Work, R. A. The availameter and its use in soil moisture control: 1. The instrument and its use. Soil Sci. **51**: 307–321. 1941.
4. Anderson, A. B. C. A method of determining soil-moisture content based on the variation of the electrical capacitance of soil, at a low frequency, with moisture content. Soil Sci. **56**: 29–41. 1943.

5. ———— AND EDLEFSEN, N. E. The electrical capacity of the 2-electrode plaster of paris block as an indicator of soil-moisture content. Soil Sci. **54**: 35–46. 1942.
6. AYERS, A. D. *et al.* The interrelationships of salt concentration and soil moisture content with the growth of beans. Jour. Am. Soc. Agron. **35**: 796–810. 1943.
7. BAVER, L. D. Soil physics. 1940.
8. BOGUSLAWSKI, E. VON. Zur Methodik des Gefässversuches bei Wasserhaushaltsuntersuchungen. Bodenk. u. Pflanzenernähr. **17**: 236–252. 1940. Biol. Ab. **15**: 2909. 1941.
9. BOUYOUCOS, G. J. AND MICK, A. H. An electrical resistance method for the continuous measurement of soil moisture under field conditions. Mich. Agr. Exp. Sta., Tech. Bull. 172. 1940.
10. BOYNTON, D. AND COMPTON, O. C. Normal seasonal changes of oxygen and carbon dioxide percentages in gas from the larger pores of three orchard subsoils. Soil Sci. **57**: 107–117. 1944.
11. BRADFIELD, R. Soil-conservation from the viewpoint of soil-physics. Jour. Am. Soc. Agron. **29**: 85–92. 1931.
12. BRIGGS, L. J. The mechanics of soil moisture. U. S. Dept. Agr., Bur. Soils, Bull. 10. 1897.
13. ———— AND MCLANE, J. W. The moisture equivalent of soils. U. S. Dept. Agr., Bur. Soils, Bull. 45. 1907.
14. ———— AND SHANTZ, H. L. The wilting coefficient for different plants and its indirect determination. U. S. Dept. Agr., Bur. Pl. Ind., Bull. 230. 1912.
15. BROWN, W. H. The relation of evaporation to the water content of the soil at the time of wilting. Pl. World **15**: 121–134. 1912.
16. BROWNING, G. M. Relation of field capacity to moisture equivalent in soils of West Virginia. Soil Sci. **52**: 445–450. 1941.
17. BUCKINGHAM, E. Studies on the movement of soil moisture. U. S. Dept. Agr., Bur. Soils, Bull. 38. 1907.
18. BURR, W. W. The storage and use of soil moisture. Neb. Agr. Exp. Sta., Res. Bull. 5. 1914.
19. CALDWELL, J. S. The relation of environmental conditions to the phenomenon of permanent wilting in plants. Physiol. Res. **1**: 1–56. 1913.
20. CAPALUNGEN, A. V. AND MURPHY, H. F. Wilting coefficient studies. Jour. Am. Soc. Agron. **22**: 842–847. 1930.
21. COILE, T. S. Soil samplers. Soil Sci. **42**: 139–142. 1936.
22. COLE, J. S. AND MATHEWS, O. R. Subsoil moisture under semi-arid conditions. U. S. Dept. Agr., Tech. Bull. 637.
23. CONRAD, J. P. AND VEIHMEYER, F. J. Root development and soil moisture. Hilgardia **4**: 113–134. 1929.
24. CRUMP, W. B. Notes on the water content and wilting point. Jour. Ecol. **1**: 96–100. 1913.
25. DAVIS, C. H. Absorption of soil moisture by maize roots. Bot. Gaz. **101**: 791–805. 1940.
26. ————. Response of *Cyperus rotundus* L. to five moisture levels. Pl. Physiol. **17**: 311–316. 1942.
27. DONEEN, L. D. AND MACGILLIVRAY, J. H. Germination (emergence) of vegetable seed as affected by different soil moisture conditions. Pl. Physiol. **18**: 524–529. 1943.
28. DULEY, F. L. Surface factors affecting the rate of intake of water by soils. Soil Sci. Soc. Am., Proc. **4**: 60–64. 1939.
29. DUNCAN, W. H. Wilting coefficient and wilting percentage of three forest soils of the Duke forest. Soil Sci. **48**: 413–420. 1939.
30. EATON, F. M. AND HORTON, C. R. Effect of exchange sodium on the moisture equivalent and the wilting coefficient of soils. Jour. Agr. Res. **61**: 401–426. 1940.

31. Edlefsen, N. E. Some thermodynamic aspects of the use of soil-moisture by plants. Trans. Am. Geophysical Union. 22nd Ann. Meeting. 917–940. 1941.
32. ———— and Anderson, A. B. C. Thermodynamics of soil moisture. Hilgardia **15**: 31–298. 1943.
33. Emmert, E. M. and Ball, F. K. The effect of soil moisture on the availability of nitrate, phosphate and potassium to the tomato plant. Soil Sci. **35**: 295–306. 1933.
34. Feustel, I. C. and Byers, H. G. The comparative moisture-absorbing and moisture-retaining capacities of peat and soil mixtures. U. S. Dept. Agr., Tech. Bull. 532. 1936.
35. Fletcher, J. E. A dielectric method for determining soil moisture. Soil Sci. Soc. Am., Proc. **4**: 84–88. 1939.
36. Furr, J. R. Is soil moisture as readily available at soil contents just above the wilting range as at field capacity? Paper presented at summer meeting of Am. Soc. Plant Physiologists. 1937.
37. ———— and Reeve, J. O. The range of soil moisture percentages through which plants undergo permanent wilting in some soils from semi-arid irrigated areas. [Unpublished, 1943].
38. ———— and Taylor, C. A. Growth of lemon fruits in relation to moisture content of the soil. U. S. Dept. Agr., Tech. Bull. 640. 1939.
39. Gardner, W. The capillary potential and its relation to soil-moisture constants. Soil Sci. **10**: 357–359. 1920.
40. Havis, L. Effect of different soil treatments on available moisture capacity of a vegetable soil. Proc. Am. Soc. Hort. Sci. **42**: 497–501. 1943.
41. Hayward, H. E. and Long, E. M. Some effects of sodium salts on the growth of the tomato. Pl. Physiol. **18**: 548–569. 1943.
42. Hendrickson, A. H. and Veihmeyer, F. J. Irrigation experiments with peaches in California. Cal. Agr. Exp. Sta., Bull. 479. 1929.
43. ———— and ————. Irrigation experiments with grapes. Proc. Am. Soc. Hort. Sci. **28**: 151–157. 1931.
44. ———— and ————. Irrigation experiments with prunes. Cal. Agr. Exp. Sta., Bull. 573. 1934.
45. ———— and ————. Responses of fruit trees to comparatively large amounts of available moisture. Proc. Am. Soc. Hort. Sci. **35**: 289–292. 1937.
46. ———— and ————. Moisture distribution in soil in containers. Pl. Physiol. **16**: 821–826. 1941.
47. ———— and ————. Irrigation experiments with pears and apples. Cal. Agr. Exp. Sta., Tech. Bull. 667. 1942.
48. Johnston, C. N. Water-permeable jacketed thermal radiators as indicators of field capacity and permanent wilting percentage in soils. Soil Sci. **54**: 123–126. 1943.
49. ———— and Atkins, O. A. An automatic plant irrigator and recorder. Pl. Physiol. **14**: 391–393. 1939.
50. Jones, I. D. Preliminary report on relation of soil moisture and leaf area to fruit development of the Georgia Belle peach. Proc. Am. Soc. Hort. Sci. **28**: 6–14. 1931.
51. Keen, B. A. The limited role of capillarity in supplying water to plant roots. Proc. 1st Int. Cong. Plant Sci. **1**: 504–511. 1928.
52. ————. The physical properties of the soil. 1931.
53. King, F. H. Textbook of the physics of soil moisture. 1907.
54. Kittredge, J. Forests and water aspects which have received little attention. Jour. For. **34**: 417–419. 1936.
55. Kramer, P. J. Effects of soil temperature on the absorption of water by plants. Science **79**: 371–372. 1934.
56. ————. Soil moisture as a limiting factor for active absorption and root pressure. Am. Jour. Bot. **28**: 446–451. 1941.

57. Lebedeff, A. F. The movement of ground and soil waters. Proc. 1st Int. Cong. Soil. Sci. **1**: 459–494. 1928.
58. Lewis, M. R. *et al.* Influence of different quantities of moisture in a heavy soil on rate of growth of pears. Pl. Physiol. **10**: 309–323. 1935.
59. Livingston, B. E. Porous clay cones for the auto-irrigation of potted plants. Pl. World **21**: 202–208. 1918.
59*a*. ———— and Koketsu, R. The water-supplying power of the soil as related to the wilting of plants. Soil Sci. **9**: 469–485. 1920.
60. Long, E. M. The effect of salt additions to the substrate on intake of water and nutrients by roots of approach-grafted tomato plants. Am. Jour. Bot. **30**: 594–601. 1943.
61. Lutz, J. F. The physico-chemical properties of soils affecting soil erosion. Mo. Agr. Exp. Sta., Res. Bull. 212. 1934.
62. Lyon, T. L. and Buckman, H. O. The nature and properties of soils. 4th ed. 1943.
63. Magistad, O. C. and Reitemeier, R. F. Soil solution concentrations at the wilting point and their correlation with plant growth. Soil Sci. **55**: 351–360. 1943.
64. Magness, J. R. *et al.* Soil moisture and irrigation investigations in eastern apple orchards. U. S. Dept. Agr., Tech. Bull. 491. 1935.
65. Martin, E. V. Effect of soil moisture on growth and transpiration in *Helianthus annuus*. Pl. Physiol. **15**: 449–466. 1940.
66. Meyer, B. S. and Anderson, D. B. Plant physiology. 1939.
67. Miller, E. C. Plant physiology. 2nd ed. 1938.
68. Moinat, A. D. Available water and the wilting of plants. Pl. Physiol. **7**: 35–46. 1932.
69. ————. An auto-irrigator for growing plants in the laboratory. Pl. Physiol. **18**: 280–287. 1943.
70. Moore, R. E. Water conduction from shallow water tables. Hilgardia **12**: 383–426. 1939.
71. Post, K. and Seeley, J. G. Automatic watering of greenhouse crops. Cornell Univ. Agr. Exp. Sta., Bull. 793. 1943.
72. Powers, W. L. Field moisture capacity and wilting point of soils. Soil Sci. **14**: 159–165. 1922.
73. Pulling, H. E. and Livingston, B. E. The water-supplying power of the soil as indicated by osmometers. Carnegie Inst. Wash., Publ. 204: 49–84. 1915.
74. Puri, A. N. Physical characteristics of soils: V. The capillary tube hypothesis. Soil Sci. **48**: 505–520. 1939.
75. Richards, L. A. The usefulness of capillary potential to soil-moisture and plant investigations. Jour. Agr. Res. **37**: 719–742. 1928.
76. ————. A pressure-membrane extraction apparatus for soil solution. Soil Sci. **51**: 377–386. 1941.
77. ————. Soil moisture tensiometer materials and construction. Soil Sci. **53**: 241–248. 1942.
78. ———— and Gardner, W. Tensiometers for measuring the capillary tension of soil water. Jour. Am. Soc. Agron. **28**: 352–358. 1936.
79. ———— and Loomis, W. E. Limitations of auto-irrigators for controlling soil moisture under growing plants. Pl. Physiol. **17**: 223–235. 1942.
80. ————, *et al.* Observations on moisture conditions in lysimeters. II. Soil Sci. Soc. Am., Proc. **4**: 55–59. 1939.
81. Russell, E. J. Soil conditions and plant growth. 7th ed. 1937.
82. Russell, J. C. The effect of surface cover on soil moisture losses by evaporation. Soil Sci. Soc. Am., Proc. **4**: 65–70. 1939.
83. Russel, M. B. The utility of the energy concept of soil moisture. Soil Sci. Soc. Am., Proc. **7**: 90–94. 1942.
84. Sachs, J. On the physiology of plants. [Eng. trans.]. 1887.

85. Schofield, R. K. The pF of the water in soil. Trans. 3rd Int. Cong. Soil Sci. **2**: 38–48. 1935.
86. Schopmeyer, C. S. Transpiration and physico-chemical properties of leaves as related to drought resistance in loblolly pine and shortleaf pine. Pl. Physiol. **14**: 447–462. 1939.
87. Shantz, H. L. Soil moisture in relation to the growth of plants. Jour. Am. Soc. Agron. **17**: 705–711. 1925.
88. Shaw, B. and Baver, L. D. Heat conductivity as an index of soil moisture. Jour. Am. Soc. Agron. **31**: 886–891. 1939.
89. Shaw, C. F. and Smith, A. Maximum height of capillary rise starting with soil at capillary saturation. Hilgardia **2**: 399–409. 1927.
90. Shive, J. W. and Livingston, B. E. The relation of atmospheric evaporating power to the soil moisture content at permanent wilting in plants. Pl. World **17**: 81–121. 1914.
91. Shull, C. A. Measurement of the surface forces in soils. Bot. Gaz. **62**: 1–31. 1916.
92. Taylor, C. A., *et al.* The wilting range in certain soils and the ultimate wilting point. Trans. Am. Geophysical Union. 15th Ann. Meeting. 436–444. 1934.
93. Veihmeyer, F. J. Some factors affecting the irrigation requirements of deciduous orchards. Hilgardia **2**: 125–284. 1927.
94. ————. Report of the committee on physics of soil-moisture. Trans. Am. Geophysical Union. 16th Ann. Meeting. 426–432. 1935.
95. ————. Report of the committee on physics of soil-moisture. Trans. Am. Geophysical Union. 17th Ann. Meeting. 318–326. 1936.
96. ————. Evaporation from soils and transpiration. Trans. Am. Geophysical Union. 19th Ann. Meeting. 612–619. 1938.
97. ———— and Edlefsen, N. E. Water in soils and its movement. Union Geodesique et Geoph. Int. Assoc. Int. D'Hydr. Sci. Bull. **22**: 355–365. 1936.
98. ————, *et al.* Use of tensiometers in measuring availability of water to plants. Pl. Physiol. **18**: 66–78. 1943.
99. ———— and Hendrickson, A. H. Soil moisture conditions in relation to plant growth. Pl. Physiol. **2**: 71–82. 1927.
100. ———— and ————. Soil moisture at permanent wilting of plants. Pl. Physiol. **3**: 355–357. 1928.
101. ———— and ————. The moisture equivalent as a measure of the field capacity of soils. Soil Sci. **32**: 181–193. 1931.
102. ———— and ————. Some plant and soil moisture relations. Am. Soil Sur. Assoc., Bull. **15**: 76–80. 1934.
103. ———— and ————. Essentials of irrigation and cultivation of orchards. Cal. Agr. Exp. Sta., Ext. Serv. Circ. 50. Revised 1936.
104. ———— and ————. Water-holding capacity of soils and its effect on irrigation practices. Jour. Am. Soc. Agr. Eng. **19**: (11). 1938.
105. ————, *et al.* Some factors affecting the moisture equivalent of soils. Proc. 1st Int. Cong. Soil Sci. **1**: 512–534. 1927.
106. Wilson, J. D. A double-walled pot for the auto-irrigation of plants. Bull. Torrey Bot. Club **56**: 139–153. 1929.
107. ———— and Livingston, B. E. Wilting and withering of grasses in greenhouse cultures as related to water-supplying power of the soil. Pl. Physiol. **7**: 1–34. 1932.
108. Work, R. A. and Lewis, M. R. Moisture equivalent, field capacity, and permanent wilting percentage and their ratios in heavy soils. Agr. Eng. **15**: 1–20. 1934.

# THE PHYSIOLOGY OF DECIDUOUS FRUITS IN STORAGE

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## INTRODUCTION

The various deciduous fruits like apples, pears, peaches and plums are living organisms, even after being separated from the parent tree at harvest time. This means that these fruits carry on physiological processes like respiration and transpiration during storage. Of course, they finally "die", and it is the job of the owner of the fruit to dispose of them long before death is reached. Just when an apple is "dead" is not easily discernible. It is true that parasitic fungi are often the cause of death, but very often old age is the cause of the "demise".

It is the obligation of the storage operator to so manipulate conditions in storage that the longest possible life of the fruit may be expected. That means he must provide conditions for controlled respiration, transpiration and possibly other physiological processes. It is the obligation of the plant physiologist to tell the storage operator what the optimum conditions for storage are.

This review purports to summarize the available information on the physiology of fruits and how it may be controlled in storage. The behavior of fruit in storage is often strongly affected by conditions in the orchard during the growing season or by the handling of the fruit by the owner after harvest. Since these pre-storage factors have a bearing on storage behavior, they will be dealt with whenever they seem pertinent.

## TRANSPIRATION

All deciduous fruits should reach the consumer while they are still crisp and juicy. Most of these fruits are 85% or more water, and even a comparatively small loss in total water content means an appreciable reduction in eating quality. By the time an apple fruit has lost 5% of its original weight, it is shrivelled enough that it not only has reduced eating quality but is unattractive because of the wrinkled appearance of the skin.

*Effect of Time of Harvest.* It has been a common observation that deciduous fruits picked in a rather immature condition shrivel more in storage than fruits picked at the proper time. For example, if Golden Delicious apples are examined in storage on February first, the fruits that were harvested on September first will show more wilting than fruits harvested October first. Because of this observation it has been assumed that early picked fruits transpire faster in storage than more mature ones.

Recent work (150) throws light on this subject with reference to apples. Whether these findings will be corroborated by other deciduous fruits remains to be seen. It was found that the rate of transpiration of apples does tend to be very high early in the growing season, but as the season progresses the transpiration rate decreases until about the normal time for harvest. The transpiration rates of several varieties of apples were found to reach their minimum shortly before the time for optimum picking maturity. After this point was reached, the apples transpired at a faster rate, especially when allowed to become over-mature on the tree. Hence it seems apparent that late picked fruits may actually transpire at a faster rate than earlier picked fruits in storage.

The fact that Golden Delicious apples examined on February first show more shrivelling if harvested early may be explained in the following ways. First, they are in storage a month longer, so it is no great wonder that the total water loss is greater. Second, during the early storage period in most cold storages, the relative humidity is likely to be rather low. This low humidity may be due to the very low refrigerant temperatures employed. It might also be due to the drying effect of the wooden containers until the vapor pressure of the wood comes to equilibrium with that of the air. Third, the temperature of these storages and of the fruit is often not so low as it is later in the season when the second lot of Golden Delicious is placed in storage.

The respiration rate of apples and pears varies with the age of the fruit, but no correlation was found between respiration rate and transpiration rate (149). As fruits grow old the rate of transpiration eventually diminishes. This is probably due to differences in the physical structure of the skin and to internal factors (170).

*Effect of Fruit Size.* Since transpiration is a surface phenomenon it is not surprising that a bushel of small apples will transpire

at a faster rate than a bushel of large apples. It has been found (149) that the transpiration rate of several varieties of apples in storage was directly proportional to the surface area of the fruit. It is recommended that transpiration results be expressed on a surface area basis rather than on a fruit weight basis as they usually are (149).

*Effect of Physical Nature of the Skin of the Fruit.* It is obvious that transpiration from fruits is unlike evaporation from a free water surface if for no other reason than that the skin of the fruit inhibits water loss. Just how much the skin of different varieties and the skin of fruit of different maturities within the same variety affects transpiration rate is not entirely clear.

It is commonly observed in the literature (26, 146) that the thickness of the skin and of the cuticle markedly affects the rate of transpiration. This is based on the observation that a variety like Golden Delicious shrivels badly in storage and that it has a thin cuticle. That the skin inhibits the transpiration rate is inescapable. It has been shown that a unit area of free water surface will evaporate 70 times more water than a unit area of the uninjured fruit of an apple per unit of time (169).

It is also true that when the waxy layer on the surface of fruits is removed by brushing or by washing with severe treatments (like sodium silicate washing), the rate of shrivelling is greatly increased (131). The importance of the nature of the surface of the fruit as it affects transpiration is also demonstrated by the effect of wax additions to the fruit in checking water loss (173).

Careful studies made on cuticle thickness and transpiration rate in apples have not always shown a good correlation (149). While it has been found that Golden Delicious did shrivel badly and also had a thin cuticle, this correlation did not hold for other varieties necessarily. Baldwin and Rhode Island Greening have the same cuticle thickness, on the average, but they transpire at different rates (149). It would seem, then, that other internal factors are sometimes more effective in determining transpiration differences.

Other skin factors that may affect transpiration rate are number and size of lenticels in the skin. It has been shown, however, that about 70% of apple transpiration is cuticular and only 30% lenticular (149). Cell wall thickness and arrangement of cells in the skin may also be factors in determining transpiration differences between varieties (26).

*Effect of Water Vapor Pressure Deficit.* The fundamental reason why fruits lose water vapor in transpiration is that there is a difference in the water vapor pressure of the fruits' internal atmosphere and in that of the surrounding atmosphere. The relative humidity of the internal atmosphere of fruits is presumably 100% under normal circumstances. Of course, after the fruits become partially desiccated, it is probably not that high. Hence if apples are held in atmospheres with a relative humidity less than 100%, water vapor is likely to move from the fruit to the surrounding atmosphere (166, 168, 171). Then, ideally, all deciduous fruits should be stored in a relative humidity of 100%. The usual recommended figure is from 85% to 90%. This recommended figure is a compromise between the ideal and the practical. If fruits are held in atmospheres saturated with water vapor, surface molds are very likely to grow on them and on their containers. These surface molds do not directly affect the fruits. The musty odor emanated by the molds is often absorbed by the fruits and contributes towards a musty flavor in them. The presence of these molds on the fruits and containers is unsightly. With a relative humidity of even 85% or 90% there is often a growth of these surface molds or "whiskers". This mold growth probably is due to the fact that the dewpoint of the fruit or containers is reached at times and there is condensation of moisture in a thin film. It is in this moist film that the molds grow. If humidities as high as 90% or 95% are used, some provision must be made for mold control. Use of ozone seems to offer some promise as a means of mold reduction in these very high humidities (198).

Relative humidity is not the only storage factor that determines the rate of water loss from fruit. Transpiration may be more rapid in a lot of fruit at 85% relative humidity at 36° F. than it is in a similar lot held at the same humidity in 32° F. air (66). This is due to the temperature factor. As the temperature rises the vapor pressure of water rises, and the difference (or deficit) between fruit and atmosphere vapor pressures is increased. Another illustration of this temperature effect is encountered when warm fruit is placed in a cold room. Let us assume that a lot of apples at 73° F. is moved into a cold storage room at 32° F. which has a relative humidity of 100%. Transpiration is relatively rapid until the fruit temperature reaches the air temperature. The water

vapor pressure of the internal atmosphere of the apples (at 73° F.) is 23.8 millimeters of mercury in this hypothetical case. The water vapor pressure of the atmosphere of the cold storage room (note that relative humidity is 100% in both cases) is only 4.6 millimeters of mercury. There is, hence, a difference or deficit of 19.2 millimeters of mercury. This deficit is about eight times as great as the theoretical deficit occurring in a situation where apples, with an internal atmosphere of 100% relative humidity, are held in air at 32° F. with a relative humidity of 50%. The most striking illustration of this effect of temperature difference, as it affects vapor pressure deficit, is seen when a rapidly transpiring plant product like lettuce is moved into storage. Lettuce removed from the field at a high temperature and placed in a 32° F. storage with a relative humidity of 100% will sometimes show wilting. Apples do not transpire rapidly enough to show this wilting, but certainly the effect on transpiration is measurable. The only apparent practical solution to this problem is to accomplish rapid cooling after fruits are placed in storage. That is, the faster the differential between room and fruit temperature is eliminated the less will be the transpiration as a result of water vapor deficit.

The foregoing discussion was based on a hypothetical situation, but actual investigation shows the soundness of the theory. It has been shown that transpiration of apples is directly proportional to the water vapor deficit in any situation (149)[1].

While more detailed studies have been conducted with apples than with any other deciduous fruit in this connection, the general effects of vapor pressure differences seem to apply to other fruits (5, 167).

There is another temperature effect on transpiration that may affect the locus of transpiration. It has been shown that if one side of an apple is colder than the other in storage, there will be a distillation of water from the warm side to the cold side, leaving the warm side withered (27). This may occur when one side of a fruit is cooled much more rapidly than the other.

*Effect of Air Movement.* It would seem logical to suppose that transpiration would be accelerated by air currents passing over fruit in storage. The magnitude of this effect is of commercial

[1] Eventually the time factor will upset this straight line relationship between vapor pressure deficit and transpiration. That is, in time skin structure may change enough with large water deficits to slow down the rate of transpiration.

interest because some storages operate with forced air circulation, others only with natural convection currents.

Several studies have shown accelerated transpiration rate of 30% to 100% when air currents of varying velocities were used with apples and grapes (5, 164). Some of these experiments are open to criticism in that the exact relative humidity around the fruits was not measured during the trials. The author has found that when fruits are subjected to different air flow rates in closed containers it is difficult to maintain the humidity at a constant level. For example, when a slow air flow rate is used, the relative humidity around the fruit is usually a little higher than the theoretical value, even though the air has been conditioned by passing it through sulphuric acid-water mixtures. Hence it is difficult to attribute differences in transpiration to velocity rates alone in studies where humidity values are not specified. Smith (165) overcame this objection by moving apples through still air at a known velocity by means of a turntable. In an early study (164) he did not specify the temperature and humidity, but in a later paper (165) on this topic he used 10° C. air at 80% relative humidity. He found increased tranpiration with apples up to a velocity of 300 centimeters per minute.

Pieniazek (149) noted that the effect of air movement on transpiration of apples was negligible, not exceeding an increase of 5%. The effect was very small when high relative humidities were used, and, of course, high humidities are recommended in cold storage practice. He used Smith's technique (165) of moving the apples through air at a known humidity.

It is sometimes claimed by storage operators that apples stored in forced air rooms show more shrivelling than apples in "still air" rooms. It has not been shown, however, that the relative humidity was identical in each case around the fruits. In the light of Pieniazek's work it would seem safe to conclude with apples, at least, that rather high velocities of air do not markedly affect transpiration if the humidity is as high as it should be. The advantages of rapid cooling with moving air would doubtless outweigh the disadvantages of slightly increased transpiration.

*Practical Implications of Transpiration Studies.* It would seem safe to conclude that ideally the smaller the water vapor pressure deficit between fruit and atmosphere the better. This principle

should apply not only during storage but while the fruit is being displayed and while in the consumer's kitchen. Certainly one of the primary causes of loss in quality is loss of moisture. The practical limitation of using very high relative humidities lies in the fact that surface molds may be troublesome. The whole problem of control of these molds should be investigated more thoroughly by pathologists. While ozone offers some promise along this line, its use may not always be practical.

Storage at temperatures as low as is compatible for best keeping of various species and varieties of fruit is certainly logical. Prompt cooling of the fruit after picking would seem to be a logical step from the standpoint of reduced moisture loss.

Use of protective coatings may be of some value in special cases for the reduction of transpiration. Additions of wax to the skin of certain varieties may pay under some circumstances (173). Use of special wraps, such as Pliofilm, Cellophane, aluminum foil or latex, may be of some practical value in this connection (13). The precaution that must constantly be kept in mind in connection with putting any "moisture proof" wrap or coating on fruits is that they must be reasonably permeable to both oxygen and carbon dioxide (13). Otherwise off flavors and physiological disorders may occur.

## RESPIRATION

No attempt will be made to discuss the nature of respiration, since that is a subject in itself (17, 18, 38, 118, 157, 180, 190). It should be emphasized, however, that when the equation $C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O +$ energy is used, it is an admitted oversimplification. There must surely be preliminary steps and side reactions involved in fruit respiration. When the full nature of fruit respiration is understood, perhaps we shall be able to do a still better job of regulating the course or rate of respiration to practical advantage. Only aerobic respiration is stressed in this review because it is of more direct interest in storage physiology. To be sure, anaerobic respiration may occur in varying degrees in fruit in storage under some circumstances.

*Effect of Age of Fruit.* Early workers (15, 58) on fruit respiration paid little attention to the effect of age. Burroughs (20) was among the first to recognize that the respiratory rate of apples is not constant at a given temperature. Later work in this country

(75) and in England (108) emphasized the marked effect of fruit maturity on respiration.

Kidd, in England (100), and later workers (119, 162), in America, showed the changes in respiration during ontogeny. Following fruit setting, the respiration rate of various apple varieties is very high. After the rate declines to a minimum, at about the time most apple varieties are harvested, the rate begins to rise again to a maximum. This respiratory peak has been called the "climacteric" by Kidd and West (98). To assign a climacteric or menopause to apples and pears seems a little far fetched, but the term has now been widely accepted by investigators all over the world. Following the climacteric, the respiratory rate declines in apples and pears and the fruits are said to be in "senescence" (100). Apples in storage are described as being pre-climacteric or post-climacteric, depending upon their position on the respiratory curve.

Changes in respiratory rate with age among stone fruits have not been studied so completely. Some studies (64, 134, 187) showed a respiratory rise after harvest, but the fruits were discarded because of decay before any decline was detected. At least one study (159) shows a decline after the climacteric was reached. One study with sweet cherries (55) showed no respiratory rise after harvest. None of these workers attached the significance to the climacteric in stone fruits that is often given to it in apples and pears. Peaches and plums are usually eating ripe by the time they reach the climacteric.

The magnitude of the respiratory rise in apples and pears seems to depend upon a number of factors, *e.g.,* species, variety, climatic conditions during the growing season, temperature of storage, and constitutents of the atmosphere in storage. The rate of respiration in Bartlett pears at 59° F. was seven times as great at the climacteric as it was at the pre-climacteric minimum (123). The rate of respiration at the respiratory peak in a variety of apples like Duchess of Oldenburg may be three times as great as at the minimum (175). In other varieties, *e.g.,* Jonathan (65) and Rhode Island Greening (175), the respiratory rise may be very small. Unpublished work by the author with McIntosh harvested from the same trees and stored over a three year period shows that this variety has a higher respiratory peak some years than others. In general, the respiratory rise is much more evident at high storage temperatures than at low (176). In fact, some varieties show no

rise in respiratory rate at a temperature as low as 32° F., even though they are found to be post climacteric upon removal from storage (176).

Figure 1 shows a typical respiration curve for McIntosh apples at harvest time. It also shows the effect of temperature, carbon dioxide and oxygen on the respiration rate of this variety while in storage and upon removal from storage.

Not only does the total amount of carbon dioxide evolved by apples vary with age, but the respiratory quotient (amount of carbon dioxide evolved divided by oxygen consumed) also varies. The respiratory quotient of one variety of apples varied from 1.0 to 1.25 at 10° C., depending upon the age of the fruit (111).

The occurrence of a respiratory rise has some significance in the storage of apples and pears, but that significance may have been over-emphasized at times. Kidd and West (101) claimed that low temperature breakdown occurred during storage in English apples only when they were placed in storage while at the respiratory peak. A similar finding was reported for the induction of soggy breakdown (also a low temperature disorder) for Grimes Golden (74). Yet no correlation between respiration rate at the time of storage and the occurrence of soft scald in Jonathan could be found (65). Both soggy breakdown and soft scald are closely related troubles, and the latter work (65) may tend to discount the earlier work with Grimes (74).

Attempts have been made to correlate the proper time of harvest of apples to be stored with respiratory rate. Kidd and West (108) reported that some varieties should be picked just before the climacteric rise begins. Phillips (148) claimed that Canadian grown McIntosh should be harvested after the climacteric. Unpublished work by the author with this variety indicates that for long time storage in New York this variety should be picked just as the rise begins. It was found that most of the apples had abscissed from the tree by the time the climacteric was passed.

The question arises as to how accurately respiration measurements made in the laboratory reflect the true respiration rate of fruit on the tree. Ezell and Gerhardt (39) studied the respiration rate of Washington grown apples five and 24 hours after picking. When they plotted the respiratory measurements made 24 hours after harvest, they noted the usual strong climacteric rise. When

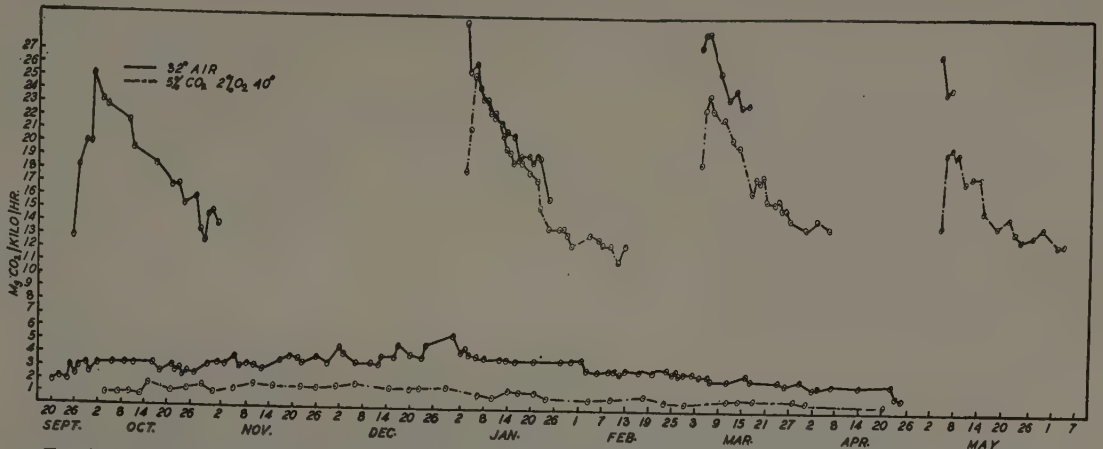


FIG. 1. Respiration of McIntosh apples in 32° F. air and 5% carbon dioxide with 2% oxygen at 40° F. (lower pair of curves). Respiration also measured at harvest time and upon removal from storage in January, March, and May (upper set of curves) at 74° F. in air (174).

measurements were made five hours after harvest on successive picking dates they did not find any such marked rise. Because they could find no sharp minimum rate prior to the respiratory rise and because they believed the usual measurements (24 hours after harvest) did not reflect the true respiratory rate on the tree, they discounted the value of this technique as an index of when to pick apples. The author believes the technique may have some value for certain varieties of apples where there is a marked minimum or a sharp rise in respiratory rate. Even though results obtained 24 hours after harvest are a physiological "artifact", if they are reproduceable they would seem to have some value in this connection. Ezell and Gerhardt (39) did not recognize that it had already been reported (112) that English apples seem to have a climacteric rise while still attached to the tree. The possibility of an artifact for certain varieties of fruit still would remain, however.

Another significant value of knowing whether or not apples are pre- or post-climacteric is in connection with a possible relation to other physiological processes. For example, post-climacteric apples and pears do not respond to ethylene additions (71, 176). Another example is that the peak in the production of volatiles seems to follow the respiratory "hump" by several days at a high storage temperature (53, 179).

*Effect of Temperature.* In general, the respiration rate of deciduous fruits increases with a rise in temperature. It has been found, however, that the respiration rate at extremely high temperatures (80° F.), or at least the softening rate, of pears is reduced (121, 181).

Most chemical reactions, according to Vant Hoff's law, increase two or three times for every 10° C. rise in temperature. The exact increase for such a temperature rise has been called the $Q_{10}$. The $Q_{10}$ for respiration seems to vary with species, variety, temperature of the storage and the nature of the atmosphere. It has been pointed out in the preceding section that the age of the fruit may also affect the $Q_{10}$. That is, one lot of McIntosh apples at 50° F. at its respiratory peak may respire faster than a second lot at 60° which is pre-climacteric.

In one of the earliest studies on apple respiration, Gore (58) found that the $Q_{10}$ of apples varied from 2.10 to 2.40, depending upon variety. Another early study (138) showed a range from

2.4 to 2.9 for different varieties of apples. Kidd and West (98, 106) found a $Q_{10}$ of 2.32 to 3.27 for English varieties in the temperature range studied. A $Q_{10}$ as high as 4.1 has been found for peaches, although the value was not that high in the higher temperature range (67).

With some plant products there is an increase in respiration after the products have been subjected to cold storage temperatures and then removed to high temperatures. Although this effect has been noted in at least one instance (21), the subsequent respiration of apples, in general, does not seem to be affected by low temperature storage (34, 75, 124, 174). An effect of 32° F. storage on the subsequent respiration rate of pears at high temperatures has been noted in at least one case (121).

*Effect of Carbon Dioxide and Oxygen.* No attempt will be made here to review all the literature on the effect of various constitutents of the atmosphere on the respiration of fruits. The discussion will be confined to those studies which seem to have direct practical application in storage practice.

Hill (81) reviewed all the early literature on the effect of certain gases on the respiration of fruits and showed the inhibition of respiration resulting from low oxygen atmospheres. Kidd and West (97, 102, 109), working in England, have done the most extensive work on this problem from the practical standpoint. Their work led to the introduction of the technique which they call "gas storage" of apples and pears. This technique involves low oxygen and higher than normal concentrations of carbon dioxide at low temperatures.

The work by Kidd and West (95, 97, 102, 107, 109) and that done later in this country in California (3, 4), New York (178, 185, 192), Iowa (151) and in Canada (42, 148, 147) can be briefly summarized as follows.

Accumulations of carbon dioxide resulting from respiration tend to slow down the respiration process in apples and pears. The reason why these accumulations retard respiration is not known. It would be logical to assume that it is merely the law of mass action operating, were it not for the fact that respiration is not a simple one step process. Thornton (186) has suggested carbon dioxide accumulation has this effect through an influence on pH of the plant tissue. It is not clear, though, whether the pH change merely ac-

companies the accumulation or directly causes a retardation of respiration.

The exact amount of carbon dioxide that can be used safely over a long storage period depends upon species, variety, temperature and possibly the section in which the fruit is grown. Pears seem to be more tolerant of carbon dioxide at low temperatures than apples (107). The effect of 5% carbon dioxide on the storage life of pears is more striking than it is on that of apples because a temperature of 34° F. can be used with the former and temperatures as high as 40° F. must be used with the latter with that concentration of carbon dioxide. Some varieties of apple, *e.g.,* Baldwin and Rhode Island Greening, when grown in New York develop browning of the flesh when as little as 5% carbon dioxide is used at 40° F. Other varieties can withstand 10% carbon dioxide at that temperature. A carbon dioxide toxicity has been noted in English and Australian varieties of apples also (14, 23). In general, toxicity is greater at low storage temperatures. For example, New York McIntosh can withstand only 2% or 3% carbon dioxide at 32° F. but can tolerate up to 15% at 45° F. Carbon dioxide injury is evidenced by a browning of the flesh in some varieties and by rough depressed areas on the skin of other varieties.

Susceptibility to a given concentration of carbon dioxide may also depend upon growing or climatic conditions in the orchard. Iowa grown Jonathan seem to be able to tolerate 5% carbon dioxide at 40° F., but New York grown Jonathan develop a type of flesh browning when stored at that temperature in that amount of carbon dioxide (151, 178).

Sometimes deciduous fruits, *e.g.,* pears or sweet cherries, are exposed to high concentrations of carbon dioxide at approximately 50° F. for comparatively short periods of time. This technique is quite properly called "carbon dioxide storage" because this gas is artificially supplied from compressed gas in cylinders or from dry ice. With this treatment various fruits, *e.g.,* pears (52), plums (160), sweet cherries (56, 194), apricots and peaches (2, 57), are kept in excellent condition for short periods. Long treatments in storage with stone fruits are likely to result in abnormal ripening (57). Not only is there retardation in respiration rate but the fungus parasites are kept at a low level of metabolic activity and hence there is less decay in transit. As much as 40% or 50%

carbon dioxide may be used in these treatments. This is in contrast with long time storage where 5% or less of carbon dioxide is used with the various fruits.

A reduction in oxygen concentration around fruits in storage has a depressing effect on respiration independent of that of carbon dioxide (102, 107). In commercial practice a concentration of 2% oxygen is often recommended for apples and pears (107, 178). The apples through their own respiration process lower the normal amount of 21% to this figure.

If oxygen levels fall below 2% for more than a few days at a time with apples, a certain amount of anaerobic respiration is likely to ensue. This probably happens not because there is no oxygen available in the atmosphere but because there is a deficiency in the fruit's internal atmosphere. It has been shown that there is a lag of from 2% to 5% in oxygen concentration inside and outside apple fruits at low storage temperatures. At high storage temperatures there may be a differential of as much as 9% between internal and external atmospheres (104).

Stone fruits do not respond favorably to long time storage in low oxygen-high carbon dioxide atmospheres (6, 43), although one worker has claimed some slight benefit with peaches (79). When held in these controlled atmospheres for long periods these fruits may have a reduced respiration rate, but secondary effects make the fruits unpalatable. They do not seem to develop their proper eating quality, and often times there is a discoloration of the flesh around the pit. Little work, however, has been done on storage of these fruits in low oxygen atmospheres in complete absence of carbon dioxide. Successful storage of these fruits for long periods in the fresh state presents a real challenge to the physiologist.

Covering fruits like apples and pears with a wax emulsion may retard respiration through its effect on carbon dioxide and oxygen (104, 189). Attempts to lengthen the storage life of deciduous fruits from the standpoint of reduced respiration by waxing is sometimes dangerous. If the artificial wax coating is too thick, oxygen may become limiting, or toxic concentrations of carbon dioxide may accumulate (172, 189). It is true that proper application of such waxes may be of some advantage from the standpoint of lengthened storage life.

*Effect of Ethylene and Acetylene.* Ethylene has been used for many years to ripen certain fruits, *e.g.,* bananas and oranges (77,

80). Its use has not ever become widespread with deciduous fruits because the problem is usually one of delaying ripening instead of hastening it. However, it is sometimes used in ripening pears (1). Ethylene effects became of considerable interest when it was found, as will be shown in a later section, that many fruits evolve it as they ripen.

Kidd and West (99) were probably the first workers to recognize the possibility of one lot of apples stimulating the respiration of a second lot of fruit. They found a sharp induction of the climacteric rise in pre-climacteric fruit when the latter were exposed to ethylene vapors or ripe apple vapors, even at low storage temperatures (99, 105, 110). The effect of ripe peaches on unripe peaches has been noted in South Africa, but only very high temperatures (90° F.) were used (91).

Later work has elaborated on the conditions under which stimulatory effects on respiration may be expected. The magnitude of the effect resulting from exposure of apples and pears to ripe fruit emanations has been known to depend upon *a*) the age of the fruit; only pre-climacteric fruits are affected by ripe fruit emanations containing ethylene (71, 176); *b*) the variety; some apple varieties show more marked respiratory response than others (176); *c*) the temperature of storage; significant effects were observed at temperatures as low as 33° F., but more striking effects were observed at higher temperatures (175, 176); *d*) the number of ripe fruits; it required as few as 1% of the total fruits in the storage chamber to stimulate a respiratory rise; *e*) the variety of the ripe fruits; some varieties seem to evolve more ethylene than others (176); *f*) ripeness of the fruit supplying the ethylene (176). In view of the foregoing conditions, the effect of one lot of apples on another may vary from nil to a very significant effect.

The possibility of removing these ripe apple emanations from the storage atmosphere so that respiratory stimulation will not ensue will be discussed in a later section.

Artificial additions of acetylene seem to have the same effect on respiration of deciduous fruits as ethylene (28, 191). Danger of explosion would seem to discourage its use where respiratory stimulation is required, however.

Suggestions have been made on the nature of the relation of ethylene production to respiration, but no complete answers seem to have been offered (69, 122, 142).

*Effect of Fruit Size.* There seems to be little information on the effect of fruit size on respiration. It is quite often stated, however, that small fruits keep longer in storage than large fruits (59, 96). It should be recognized that factors other than respiration may be involved with the size factor. For example, small apples are usually firmer when placed in storage than large apples.

The author has conducted two experiments on the effect of fruit size with McIntosh apples and found a suggestion of more rapid respiration with large apples. The effect of fruit size should be studied further to discover the effect of exact leaf-fruit ratios on the tree on respiration in storage. From this preliminary work it would appear that respiration is not nearly so much a surface phenomenon as is transpiration (149).

*Effect of Culture and Climate.* Several studies (29, 94) have shown that the respiration rate of apples in storage was increased by application of nitrogen fertilizers to orchard trees. One study (59) indicated no response in respiration of fruit during the growing season, even though the nitrogen content of the fruit was markedly increased by nitrogen applications in the orchard. It would seem that, if conclusions were to be made on the effect of nitrogen fertilizers on keeping quality, the respiration measurements should be made during storage. Hulme (87) found an increased respiration rate of apples in storage after injecting individual limbs with urea. The author has sprayed individual limbs of Rhode Island Greening trees during the summer with urea solution and found an effect on respiration. He has also found a number of instances of increased respiration after harvest in McIntosh after applications of nitrogen fertilizer had been made in the orchard.

In one study in which it was not clear whether a definite potassium deficiency existed in the trees, an application of potassium fertilizers had no effect on subsequent respiration of apples in storage (29). Wallace (195) reviewed a considerable amount of literature and concluded that there was no clear-cut relation between mineral constitutents of apples and their potential storage life.

The exact effect of climate during the growing season on the respiration rate of apples or pears in storage has not been fully explored. Studies by the author indicate marked fluctuations in rate of McIntosh respiration picked from the same trees from year to year. One worker (197) has claimed that low respiration rate

in storage was correlated with warm dry weather during the few weeks preceding harvest. One investigation with pears (161) showed a higher respiratory activity with pears on dry plots than fruits picked from irrigated plots, but there was no reduction in storage life in fruits from the dry plots. Effects of climate on keeping quality of fruits can not be correlated solely with respiration, since climate may also affect firmness of the fruit, susceptibility to storage disorders and possibly other fruit characteristics.

*Effect of Injury.* Many plant tissues respire faster when wounded. Most studies have shown little effect of bruising of apples on respiration rate (31, 92), but skin punctures or cutting the fruit does seem to stimulate respiratory activity (92). The author has examined the effect of bruising on McIntosh apples and has found no significant effect, whether or not they were bruised in the pre-climacteric or post-climacteric condition.

Severe injury to the cells of fruits, as may be caused by freezing followed by thawing, is very likely to induce a rise in the respiration rate (25).

*Effect of Relative Humidity.* It has been found (149) that the relative humidity of the atmosphere did not affect the respiration of apples unless the humidity became very low. This reduction in respiration could be attributed to physical changes in the character of the skin of the fruit which accompanied shrivelling. One worker (120) has reported increased respiration rate of pears when low humidities were used. Later work has indicated that the effects he noted were probably due to the very high temperature employed rather than the low humidity (181). Differences in relative humidities in the higher ranges (70%–100%) seem to be ineffectual in affecting respiration rate because the humidity of the intercellular spaces of the fruits probably stays close to saturation until the apples become somewhat desiccated.

*Heat of Respiration.* Some of the studies made on heat of respiration values were done by calculating the heat energy evolved by complete oxidation of a hexose sugar (67). Other studies have used calorimeters and measured the heat evolved (60, 61, 83, 163). The most exhaustive work on this subject has been performed by Green, Hulkill and Rose (60). They found that a ton of Stayman Winesap apples at 45° F. would evolve about 1550 BTU per 24-hour period. They also calculated the theoretical heat loss on the

basis of oxidation of a hexose sugar and found fairly good agreement (less than 10% error). That is, it would seem that most of the energy lost in respiration is lost as heat.

A complete table of heat of respiration values for various fruits is available (158). Studies on heat of respiration should not overlook the fact that the heat evolved may vary with age of the fruit as well as the variety. Not even the variety is always specified (158). It should also be recognized that the $Q_{10}$ is not a constant for even a given variety. Heat of respiration studies are still in progress, and eventually they will probably include the effects of these other variables.

A knowledge of the magnitude of heat of respiration is of utmost value to the refrigeration engineer who must compute refrigeration requirements. The author has used the figures of Griffiths and Awberry (61) and calculated the rise in temperature of apples in storage. Assuming that there is no heat loss (as there inevitably would be), a bushel of apples at 32° F. would raise their own temperature one degree F., in four days. At 66° F. the fruits would raise their own temperature two degrees in 23 hours. With more rapidly respiring fruits, like peaches, these temperature rises would be even larger. Calculations of this type are open to the criticisms noted above, but they illustrate the magnitude of the heat production that the engineer must deal with.

*Relation of Respiration Rate to Length of Storage Life.* Often there is a good correlation between respiration rate of apples and pears and softening and general storage life (26, 94), but frequently there doesn't seem to be a good correlation because of other factors limiting the length of storage life (161). Kidd and West (96) have gone so far as to forecast the potential storage life of an apple from a knowledge of the height of the climacteric rise, date of the rise, and the general level of respiration. The author (174) has found that the marketable life of McIntosh, as grown in New York, was at an end when this variety had evolved between 17.5 and 19.5 grams of carbon dioxide per kilogram of fruit when harvested each year at the same point on the respiratory curve. This represents an error of about 10% when complicating factors like low temperature breakdown were excluded.

It may be concluded that the respiration rate of deciduous fruits is one of the best single indices of metabolic activity that we have.

It should be recognized, however, that other factors such as transpiration, low temperature disorders and fungal invasion may be the determinants of length of storage life. A given lot of fruit may actually respire faster than a second lot, but because it is firmer at the start of the experiment it may have a longer storage life (161).

*Practical Implications of Respiration Studies.* Deciduous fruits do not respire at a constant rate at any one temperature. Whether this variation in rate can be used to practical advantage in determining when to pick certain varieties for storage remains to be seen. It would seem to be of doubtful value with some varieties but may prove to be of use with others.

The effect of a lowering of temperature on the respiration rate of fruits is the fundamental principle involved in cold storage. Many apple varieties will keep twice as long at 32° F. as they will at 50° F.

Retardation in the respiration rate of apples and pears by the use of relatively high concentrations of carbon dioxide and low concentrations of oxygen at a comparatively low storage temperature is the basis of the technique called "controlled atmosphere storage". This procedure has real commercial possibilities with certain species and varieties but not with others. One of the values of this newer storage technique is that there is a residual effect of storage. That is, apples removed from controlled atmosphere storage respire slower on the market place or in the hands of the consumer than do similar apples removed from cold storage (174). It is as though the fruits had been anesthetized during storage and never wholly recovered from the anesthetic.

When relatively high concentrations of carbon dioxide are used around fruits like pears and sweet cherries for comparatively short periods the treatment is called "carbon dioxide storage". Most sweet cherries now shipped from the West Coast are sent with this treatment in transit. Carbon dioxide storage differs from controlled atmosphere storage in that the carbon dioxide is added artificially, there is no control of oxygen, and the period of treatment is relatively short. Carbon dioxide storage would hardly seem to be an appropriate term for long time storage for a variety of apples like Rhode Island Greening where no carbon dioxide is used but the oxygen level is kept very low.

Evolution of ethylene by ripe fruits may significantly shorten the storage life of less ripe fruits stored with them. Where conditions are favorable for such an effect, as much as 25% of the storage life of a given lot of apples may be lost because of the presence of the ripe fruits.

The effect of culture and climate on respiration rate has not been fully explored. Under some conditions there may be measurable effects of variations in culture and climate on keeping quality.

The heat evolved in respiration is a very important factor for the refrigeration engineer. Heat of respiration must be compensated for in both precooling and storage of various fruits. Variations in heat produced within a species of fruit should be studied further with regard to variety differences and age of fruit.

### PRODUCTION OF ORGANIC VOLATILE MATERIALS

*Ethylene.* Elmer (35) was probably the first to report that apples as they ripen emanate a gas that has effects similar to that of ethylene. Later work confirmed this report (72, 99, 105, 175, 176, 179). It has been shown that a sufficient amount of this gas is included in organic apple emanations to stimulate the respiration rate of other apples (99, 105, 175, 176, 179). The particular gas in these emanations responsible for these effects has now been definitely identified as ethylene (46, 47, 49, 72). Ethylene seems to be evolved not only by apples but by pears (50, 70, 72), peaches and plums (89, 90, 91) as they ripen.

Quantitative studies of ethylene production by apples and pears as they ripen (69, 140, 141, 142) have been made. In apples there is a progressive rise in the quantity produced to a peak followed by a decline in production. In McIntosh apples the peak seems to follow the respiratory peak by five days at a temperature of 20° C. (142). In pears the production curve seems to follow the respiratory curve very closely, the peak in production of carbon dioxide and of ethylene occurring at about the same time (69). Varieties of apples (141) and pears (69) having a long storage life seemed to produce less ethylene than those with a short storage life. One apple produced approximately one cubic centimeter of ethylene during its life after harvest (46). With pears it was found that the maximum amount of ethylene was produced at 20° C. with none being produced at 40° C. (69). Low oxygen atmospheres seem to markedly inhibit production of ethylene by pears (69).

Since complete absence of ripe fruit in the storage room is not always practical, the question arises as to the possibility of removing these organic apple emanations containing ethylene. Ventilation is not practical because of the extreme cost of refrigerating vast quantities of fresh air during the critical fall months of storage. Probably the first one to attempt air conditioning from this standpoint was Fontanel (44). He claimed success in removing the gas responsible for stimulating ripening of "fruit" by air conditioning with activated carbon. Repetition of this work with both lignite and cocoanut shell carbon did not show any promise in the high humidities involved in apple storage (176, 179). The work of Southwick (179) suggested the possibility of adsorbing bromine on the surface of activated cocoanut carbon, and air conditioning to remove ethylene. Air conditioning with this technique on small scale lots of apples works perfectly; only time will tell if this procedure has commercial possibilities (176). In testing the effectiveness of an ethylene absorbent or adsorbent the epinasty test (30) is very useful. Tomato plants are extremely sensitive to small concentrations of ethylene. Where air conditioning is not completely effective in removing the ethylene evolved by ripe fruit, tomato plants will show epinasty within a few hours at relatively high temperatures. This test has been used to considerable advantage by the author.

There is some evidence to the effect that ethylene may accumulate in toxic amounts in apple storage. The result is spotted fruit (113, 175).

*Other Volatile Materials.* While ethylene is one of the principal constituents of the emanations of deciduous fruits, there are other organic volatiles (196).

The odorous constituents of apples have been identified as consisting of the amyl esters of formic, acetic, caproic and caprylic acids as well as geraniol (154, 156). In peaches the odorous materials have been identified as linalyl esters of formic, acetic, valeric and caprylic acids. A high molecular weight aldehyde and an essential oil have also been isolated from the gases responsible for the odor of peaches (155). As yet, no studies have been made on the progressive changes of the various fractions of these odorous gases as the fruits ripen. The odorous substances are presumably produced in maximum amounts when the fruits are eating ripe.

Acetaldehyde has been identified as a constituent of apple and pear flesh (40, 51, 54, 76, 85, 135, 154). There seems to be more of this aldehyde in pear flesh than in apple (51). The exact role of acetaldehyde in fruit metabolism is not yet fully understood, although the suggestion has been made that it is present as a normal intermediate product of respiration (41). Most investigators of this topic seem agreed that there are traces of this aldehyde in normal apple and pear flesh and that during senescence (143) or in low oxygen atmospheres (182) or in fruits affected with apple or pear scald (51, 76, 183) there may be accumulations. The suggestion that a disorder like pear scald may be caused by accumulations of acetaldehyde (76) has been challenged by at least one investigator, Trout (188), who has pointed out that these accumulations may not necessarily be the cause of scald but may merely accompany the disorder.

Traces of ethyl alcohol have been found in normal pear and apple flesh (40, 135, 182), but it is not likely that appreciable quantities accumulate except under very low oxygen conditions (182) or during senescence (143). Vapors of ethyl alcohol in fruit tissue seem to retard respiration (103). It is very likely that the off flavors encountered in fruit that has been stored in anaerobic conditions or that has developed flesh breakdown from one cause or another is due to ethyl alcohol or acetaldehyde, or both (51).

The only specific gases emanating from fruits that have been measured quantitatively are ethylene and acetaldehyde. Measurements have been made of total volatiles and we know little of the quantitative or qualitative production of the various volatiles other than ethylene and acetaldehyde (45). Measurement of these total volatile materials is usually made by adsorption in sulphuric acid followed by oxidation of ceric sulfate (51, 179). Ethylene is not included in these measurements unless "activated" sulphuric acid (silver and nickel sulfates added) is used (51). Sometimes total volatiles are determined by complete combustion of the gases following removal of carbon dioxide evolved in respiration (48). While these measurements of total volatiles are valuable they would be more so if the quantities of constituent gases were known For example, the total quantity of volatiles might be quite low, yet a specific volatile responsible for some disorder (such as apple

scald) might be present in considerable quantities from a relative standpoint.

Measurement of total volatile materials emanating from apples has shown that temperature has a very striking effect. With Golden Delicious apples almost twice as much was produced at 36° F. as at 31° F. (53). With McIntosh apples twice as much was produced at 40° F. as at 32° F. (179). It has been noted that there was a residual effect of storage treatment on the subsequent evolution of total volatiles. It was found that McIntosh apples stored at 32° F. evolved less total volatiles when removed to a high temperature than did similar apples which had been held in 40° F. storage (179). This finding may offer a clue as to why McIntosh apples held in cold storage never seem to develop their full aroma. The same thing has been observed with McIntosh apples held in controlled atmosphere storage as compared with storage in air (179). While it is true that controlled atmosphere apples may not be as aromatic as apples of the same degree of ripeness held in ordinary cold storage, they are longer lived upon removal from storage and evolve volatiles over a longer period of time. The fact remains, however, that they are not so aromatic as cold storage apples upon removal from storage.

Injured fruit seems to produce volatiles more rapidly than uninjured fruit (53). Whether this fact has any significance from the standpoint of loss of quality as a result of injury remains to be shown.

*Practical Implications of Organic Emanation Studies.* It has been pointed out previously that sufficient ethylene may be evolved from one lot of fruit to stimulate the ripening of other fruits. The practical value of ethylene removal from fruit storages has not yet been demonstrated.

The storage disease of apples called "scald" is caused by accumulations of certain gases around the fruits. These gases are evolved by the fruits themselves. The exact gas or gases responsible for this disease are not yet known. Their identification would help considerably in a better approach to control of the disorder. Attempts at control are now made by wrapping or mixing the fruit with paper impregnated with mineral oil. The possibility of air conditioning for removal of these noxious gases should be explored.

The organic emanations that contribute aroma are of considerable importance from the standpoint of fruit quality. The storage

treatments that are most likely to give maximum production of these aromatic constituents as well as long keeping have not yet been very thoroughly investigated.

## CHEMICAL CHANGES DURING STORAGE

*Enzyme Action.* Many of the chemical changes occurring in fruits during storage can be attributed to enzyme action. For example, the change from starch to sugar, sucrose to invert sugar, or of proto-pectin to pectinic acid is due to enzyme action. However, very little work has been done on enzymes as such or their specific responses to changing storage conditions. The experimental work has concerned itself with the net result of these enzyme reactions. For example, in studying the softening of fruits in storage, the investigational work has concerned itself with increases in pectinic acid rather than in studying the specific activity of the protopectinase enzyme. The results of some of these enzyme actions are discussed in the sections to follow.

Some work has been done on oxidase and catalase activity in apples and pears in relation to their keeping quality in storage. With pears it was found that the curve for catalase activity was U-shaped. The minimum rate of catalase activity was found to occur at or near the time the Bartlett pear should be harvested for storage. There was a subsequent rise in catalase activity after this minimum point was reached (37, 38). There was a more or less continuous declining rate in oxidase activity in pear fruits throughout the whole growing season. Oxidase activity in pears continued to decline in rate during storage (37, 38). In apples it has been found that there is a continuously rising catalase activity during the growing season and after harvest. Oxidase activity was found to decrease during the growing season and might or might not increase when the fruit becomes more mature. Fruit harvested when fully mature usually showed a higher catalase activity and a lower oxidase activity in storage than fruit picked when less mature (39). The full significance of oxidase and catalase activity has not been established for fruits in storage. It seems that in apples and pears oxidase and catalase activity have no apparent direct relation to respiration or to each other (39).

*Sugars.* The major portion of the dry matter of deciduous fruits is made up of carbohydrate material. Of this carbohydrate ma-

terial sugars compose the largest fraction. The sugars commonly found in these fruits are glucose, fructose and sucrose (184). The exact proportion of each depends upon species and to some extent upon variety and maturity (184). For example, fructose and glucose are the principal sugars in apples and pears whereas sucrose is the principal one in peaches (132, 184). The amounts and proportions of these sugars also vary in different parts of the fruit (73). For example, in pears fructose is the main sugar in the flesh whereas dextrose is the main sugar in the skin (132). The blushed side of fruits is usually higher in total sugars than the unblushed (shaded) side (12). Fruits vary in their concentrations of total sugars from year to year and from orchard to orchard (10).

The usual procedure in apples is for the total sugars to increase for a time during storage and then to begin to decrease (10, 78, 82, 126). Increase in total sugars during the early stages of storage is due to hydrolysis of starch (11) in apple, and in pear it is probably due to a breakdown of sorbitol (115, 133). The normal sugar changes can in a general way be retarded by lowering the storage temperature (126) or by modifying the atmosphere (136, 137). Ethylene treatment of preclimacteric fruit tends to cause an accelerated loss of sugar through respiration (32). It is very difficult, however, to always correlate storage treatments with sugar changes in so far as total amounts are concerned (126). During storage there is apparently considerable conversion from glucose to fructose or possibly *vice versa,* particularly during senescence (11, 145).

There have been some attempts to correlate carbohydrate composition with potential storage life but they have not always been convincing. For example, it has been claimed that when the nitrogen content of the apple fruit was high, sugar and acid losses were more rapid in storage (10). It was also predicted that when sucrose content is high in apples and nitrogen low, storage life will be longer (78). It may some day be definitely established that carbohydrate composition has a definite relation to potential storage life, but it will probably still be recognized that other factors may be the determinants.

One of the causes of death of fruits is often presumed to be lack of respirable material. For example, it has been stated that exhaustion of the sucrose content of apples coincides with death of the fruit (78). However, there are reports that fructose is the

respirable material in apples and that there is a conversion of glucose to fructose even during senescence (144, 145). Another debatable point that arises here is—just when is an apple "dead"? The author has noted that there may be as much as 8% total sugars left in apples when they are in a degenerated condition long past the state of marketability.

*Starch.* Many varieties of apples and pears have starch in the tissues of the flesh (1). It has been reported that some varieties have as much as 1% when placed in storage (11). During storage this is converted into sugars, as noted above. The presence of starch in stone fruits during storage has not been reported.

*Acids.* During storage of deciduous fruits there is a gradual loss in total acidity (33, 78, 93, 126) and a rather small increase in pH (22, 93). The acid involved is primarily malic, although there have been some reports of traces of tartaric, citric and succinic acids in deciduous fruits (16, 139). Bigelow and Dunbar (16) offer a full bibliography on the work on fruit acids up to 1917 and offer data on the percentages of acids in the common fruits. Acids decrease during storage presumably because they are a partial substrate for respiration (126).

Various workers have tried to associate acid content or acid changes with the storage life of fruit. One report (33) claims that the ratio of total acids to dissociated acids determines the keeping quality of fruits in storage. Another (62) claims that internal breakdown in apples is associated with high acidity. This worker (62) recommends that in view of this fact apples should have a period at high temperatures to reduce the acid content of the fruit before low temperature storage. This recommendation based on theory is not in accord with the observed facts in connection with general longevity of fruits. It is quite possible, however, that fruit acidity may have some bearing on specific storage disorders. It has been shown, for example, that the amount of the storage disorder called Jonathan spot was directly correlated with the amount of acid (152). There was more Jonathan spot on samples entering storage with a low acidity and on samples which lost the smaller amounts of total acid during storage (152). The authors also found a small amount of soggy breakdown when the total acid loss was small in storage. How much these correlations are pure coincidence and how much a cause-effect relationship is not clear as yet.

Attempts to correlate storage treatments with acidity changes have not given very promising results in experimental storage work (93, 126), although, in general, storage in high temperatures results in more rapid acidity losses (152).

*Pectin.* As deciduous fruits ripen in storage there is a change from proto-pectin to pectin. This pectin change is usually offered as one of the primary reasons for softening of fruits (7, 24). As the proto-pectin is dissolved away from the middle lamella, the cells of the flesh become less firmly cemented together and softening ensues. Various workers (7, 24, 121, 153, 177) have found a good correlation between fruit softening and increase in pectin. When fruits become over-ripe, pectin reaches its highest percentage and then declines in amount. There is a very rapid disappearance of this soluble pectin or pectinic acid in over-ripe apples (192). Whether it breaks down into its component parts is not known, but it presumably does. If it does, it may partially account for the fact that the sugar content of over-ripe fruits is often unexpectedly high.

Soluble pectin increases can usually be rather closely correlated with storage treatments. For example, the increase is very much diminished by low temperature storage (121) or by controlled atmosphere storage (36, 177, 193). While there is normally a more rapid increase in pectin at higher temperatures, if the temperature goes too high (80°) there is a retardation in activity of the protopectinase enzyme that produces water-soluble pectin (121). The softening rate decreases also at these very high temperatures with pears (121, 181). Sometimes the storage treatment has a residual effect on subsequent pectin changes in certain fruits. In apples it has been observed that controlled atmosphere treated fruits do not soften as fast as would be expected upon removal to air at high temperatures and that protopectin hydrolysis is slower than would be expected (193). In plums the normal pectin increase at high temperatures seemed depressed after storage at low temperatures in one study (68).

In stone fruits the softening rate is very rapid and the pectin or pectinic acid increase is normally so, too (7, 177), but attempts to correlate differences in rate of softening between varieties on a basis of this factor have not been altogether successful (64). Obviously there must be other factors involved in softening besides merely the pectin transformations. Differences in morphology and anatomy possibly would help to explain varietal differences in softening rate.

*Waxes.* On the outer surface of the epidermis of the apple fruit there is a layer called the cuticle. Considerable soft wax may develop on the surface of this cuticle. This waxy coating has been found to consist of ursolic acid, "oily fraction" and "total ether soluble extract". An ether extract does not contain a ketone in appreciable amounts, but the bulk of the extract in apples and pears contains n-nonacosane (127, 128). During storage of apples all these constituents increase in amount, but the oily fraction increases at a faster rate than the ursolic acid (129). This shift in amount and proportion of oily fraction probably accounts for the increasingly greasy feeling and appearance of some varieties of apples in storage. The total amount of cutin also increases during storage of apples (130). Different varieties of apples vary widely as to their amounts of ursolic acid, oily fraction and total ether extract (129), and the amounts vary within varieties from season to season and from orchard to orchard (129, 130).

Several workers (127, 146) have attributed variations in physiological processes to variations in the nature of the waxy coating of fruit, but the full relation of this factor to the physiology of the fruit has not been very fully explored as yet.

*Nitrogen.* Changes in the total nitrogen in the flesh of apples does not change very much during storage, but there is a marked change in the protein fraction (8, 9, 86). The insoluble (protein) nitrogen increases in amount. This increase in apples and pears follows the respiratory rise very closely (114). The increase in protein nitrogen is due to a decrease in soluble nitrogen (86). The rise in amount of protein nitrogen can be induced in preclimacteric fruits by addition of ethylene, or it can be delayed by use of controlled atmosphere storage (114). While storage treatments may be correlated rather well with protein nitrogen changes, it does not seem likely that determinations of this change would be as valuable as respiration measurements, because the magnitude of protein differences is not so marked as respiration differences (88).

Attempts to correlate the content of total nitrogen with keeping quality of fruits in storage have given conflicting results. Several English workers (9, 86, 87) have associated poor keeping quality with high nitrogen. The work of Gourley and Hopkins (59) typifies most of the work in this country which shows no relation between fruit nitrogen and keeping quality. Investigations on the McIntosh variety of apples by D. Boynton and the author (un-

published) show that differential nitrogen treatments in the orchard may show no effect on keeping quality because the amounts of nitrogen in the tree may not be affected. When different levels of leaf nitrogen (sampled in July) were attained, there was a strong suggestion of reduced fruit firmness and ground color (yellow) development with the higher nitrogen applications in the orchard. When leaf nitrogen was high there was a tendency for greater susceptibility to brown core (a low temperature disorder) in this variety. This variety is very sensitive in other ways to nitrogen level differences, so it does not necessarily follow that these findings will apply to other varieties.

*Ash.* There are not marked variations in the ash content on a dry weight basis of fruits as they ripen in storage (19). There have been some attempts to correlate storage life with amounts of mineral constituents in the fruit. For example, one report (19) claimed that long keeping of apples was associated with high potassium and phosphorus in the fruit. Other reports (29, 84) have shown no correlation between mineral content of apples and storage life. It is true that a real deficiency of a mineral like potassium (195) might affect the storage life of fruits, yet Wallace (195) points out that high potassium fruits may keep better than low potassium fruits at low temperatures and poorer at higher storage temperatures. He concluded that there was no clear cut relation between mineral composition and length of storage life.

*Practical Implications of Studies on Chemical Changes.* Studies on chemical changes occurring in storage have helped us understand the effect of storage treatments on softening. Methods of retarding the proto-pectin to pectin change is sought by all storage investigators. In general, attempts to correlate other chemical changes with specific storage treatments have not been very fruitful from a practical standpoint. Effects of storage treatment on chemical changes that affect quality have not been explored so fully as they might have been. While some work has been done on the effect of storage treatment on vitamin changes, comparatively little has been performed as yet on the general nutritional value of various fruits when stored in different ways.

## SUMMARY

The transpiration rate of deciduous fruits determines how soon a given lot of fruits will become unmarketable because of shrivelling

or wilting. This loss of water results not only in a loss of eating quality but also in unsightly appearance of the fruit. The transpiration rate is influenced by the vapor pressure deficit, air movement and certain internal fruit factors. Transpiration may be held at a very desirable minimum by storage in relative humidities approaching saturation, but surface growing fungi are likely to be a source of trouble. Work on methods of control of these surface molds by plant pathologists is needed.

The respiration rate of deciduous fruits is probably the best single index of metabolic activity in relation to potential storage life. It should be recognized that respiration rate is not the sole determinant of length of keeping of these fruits, however. The respiration rate of a given lot of fruit in storage depends upon its age, climate during the growing season, temperature, carbon dioxide and oxygen level, and ethylene concentration. It is not entirely clear what the effects of bruising, fruit size and nitrogen level in the tree are on subsequent respiration of fruits in storage. While considerable work has been done by physiologists on the nature of plant respiration, still more work is needed. When the complexities of fruit respiration are fully understood it is very possible that the pomologist can suggest better ways of handling fruits in storage. For example, one of the greatest challenges offered to the physiologist in this connection is that of finding a way to reduce the metabolic activity of stone fruits without incurring unfavorable secondary reactions. This would permit long time storage in the fresh state.

Production of organic volatile emanations by deciduous fruits is of considerable interest to the pomologist. Under some circumstances, one lot of apples or pears may evolve enough ethylene to stimulate the ripening of a second lot in storage. The odorous emanations of various fruits are of considerable importance from the standpoint of eating quality. Not very much is known about ways in which maximum aroma may be produced without unduly sacrificing length of keeping in storage. Accumulations of certain volatile materials, as yet unidentified, cause a storage disorder known as "scald" on many varieties of apples.

Deciduous fruits undergo many chemical changes as they ripen. Many of the analyses of the various constituents of these fruits have not been of great benefit in interpreting experimental results in storage. A notable exception is that of the proto-pectin to pectinic acid

change which accounts at least in part for the softening of fruits in storage.

Improvements in storage techniques are the responsibility of the physiologist, the pathologist, and the refrigeration engineer. Not only must studies of normal metabolism be continued, but causes of pathogenic or physiogenic disorders must be constantly investigated. Tremendous economic loss is caused by these disorders in storage.

LITERATURE CITED


1. Allen, F. W. Physical and chemical changes in the ripening of deciduous fruits. Hilgardia **6**: 381–441. 1932.
2. ———. Carbon dioxide investigations: influence of carbon dioxide atmospheres upon cherries, plums, peaches and pears under simulated transit conditions. Am. Soc. Hort. Sci., Proc. **37**: 467–472. 1939.
3. ———. Influence of carbon dioxide in lengthening the life of Bartlett pears. Am. Soc. Hort. Sci., Proc. **37**: 473–478. 1939.
4. ———. Carbon dioxide storage for Yellow Newton apples. Am. Soc. Hort. Sci., Proc. **40**: 193–200. 1942.
5. ——— and Pentzer, W. T. Studies on the effect of humidity with cold storage of fruits. Am. Soc. Hort. Sci., Proc. **33**: 215–223. 1936.
6. ——— and Smock, R. M. Carbon dioxide storage of apples, pears, plums and peaches. Am. Soc. Hort. Sci., Proc. **35**: 193–199. 1938.
7. Appleman, C. O. and Conrad, C. M. Pectic constituents of peaches and their relation to softening of the fruit. Md. Agr. Exp. Sta., Bul. 283. 1926.
8. Archbold, H. K. The nitrogen content of stored apples. Ann. Bot. **39**: 97. 1925.
9. ———. The chemical studies on the physiology of apples. II. The nitrogen content of stored apples. Ann. Bot. **39**: 97–107. 1925.
10. ———. Chemical studies on the physiology of the apple. IX. The chemical composition of mature and developing apples and its relationship to environment and to the role of chemical change in store. Ann. Bot. **42**: 541. 1928.
11. ———. Ripening processes in the apple and the relation of time of gathering to the chemical changes in cold storage. Ann. Bot. **46**: 407–459. 1932.
12. ——— and Barker, A. M. Physiology of apples; chemical studies. Ann. Bot. **48**: 957–966. 1934.
13. Baghdadi, H. A. and Smock, R. M. The comparative value of certain plastic materials and waxes in checking moisture loss from apples. Am. Soc. Hort. Sci., Proc. **42**: 238–246. 1943.
14. Barker, J. and Kidd, F. Injury to Australian apples due to carbon dioxide at low temperatures. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1934: 109–110. 1935.
15. Bigelow, W. D. *et al.* Studies on apples. Part I. Storage, respiration, and growth. U. S. Dept. Agr., Chem. Bul. 94. 1905.
16. ——— and Dunbar, P. B. Acid content of fruits. Jour. Ind. & Eng. Chem. **9**: 762–767. 1917.
17. Blackman, V. H. Some biological aspects of the storage of fruits. Sci. Prog. **33**: 417. 1939.
18. ——— and Panja, P. Analytical studies in plant respiration. I. The respiration of a population of senescent ripening apples. Royal Soc., Bot., Proc. **103**: 412. 1928.

19. Brown, J. W. Chemical studies in the physiology of apples. XI. The relation between the mineral constituents of apples and the soils on which they are grown. Ann. Bot. **43**: 817. 1929.
20. Burroughs, A. M. Changes in the respiration rate of ripening apples. Am. Soc. Hort. Sci., Proc. **19**: 225–234. 1922.
21. ————. Studies in apple storage. *In* Storage Investigations, Marble Lab. Inc., Rep. **3**: 101–138. 1923.
22. Caldwell, J. S. Hydrion concentration changes in relation to growth and ripening of fruits. U. S. Dept. Agr., Tech. Bul. 403. 1934.
23. Carne, W. M. and Martin, D. The influence of carbon dioxide concentration on brown heart and other storage disorders. Jour. Coun. Sci. & Ind. Res. [Australia] **11**: 47. 1938.
24. Carré, M. H. An investigation of the changes which occur in the pectic constituents of stored fruits. Biochem. Jour. **16**: 704. 1922.
25. Carrick, D. B. The effect of freezing on the respiration of the apple. Cornell Agr. Exp. Sta., Mem. 110. 1928.
26. Cummings, M. B. and Lombard, P. M. Farm apple storage. Vt. Agr. Sta., Bul. 186: 99–136. 1915.
27. Curtis, O. F. Vapor pressure gradients, water distribution in fruits and so-called infra-red injury. Am. Jour. Bot. **24**: 705–710. 1937.
28. Davies, R. and Boyes, W. W. Pre-storage treatment of Kelsey plums with acetylene and ethylene. So. Africa Dept. Agr., Low Temp. Res. Sta. Rep. 1938–39. 31. 1940.
29. Degman, E. S. and Weinberger, J. H. Studies on firmness and keeping quality of certain fruits. Md. Agr. Exp. Sta., Bul. 366. 1934.
30. Denny, F. E. and Miller, L. P. Production of ethylene by plant tissues as indicated by the epinastic response of leaves. Boyce Thomp. Inst., Contr. **7**: 97–102. 1935.
31. Drain, B. D. Temperature and respiration enzymes of apples. Bot. Gaz. **82**: 183–194. 1926.
32. Dustman, R. B. Effect of ethylene, ethylene chlorohydrin, and ultra violet light on carbohydrate content of stored apples. Pl. Physiol. **9**: 637–643. 1934.
33. DuToit, M. S. and Rayneke, J. Studies in the keeping quality of fruit. Union So. Africa Univ. Stellenbesch, Bul. 118. 1933.
34. Eaves, C. A. Preliminary study of the effect of a series of temperature changes upon respiratory activity of apples during the post-climacteric in senescent apples. Sci. Agr. **16**: 28–39. 1935.
35. Elmer, O. H. Growth inhibition of potato sprouts by volatile products of apples. Science **75**: 193. 1932.
36. Emmett, A. M. An investigation of the changes which take place in the chemical composition of pears stored at different temperatures with special reference to pectic changes. Ann. Bot. **43**: 269–308. 1929.
37. Ezell, B. D. and Gerhardt, F. Oxidase and catalase activity of Bartlett pears in relation to maturity and storage. Jour. Agr. Res. **56**: 337–346. 1938.
38. ———— and ————. Respiration and oxidase and catalase activity of apple and pear fruits. Jour. Agr. Res. **56**: 365–386. 1938.
39. ———— and ————. Respiration and oxidase and catalase activity of apples in relation to maturity and storage. Jour. Agr. Res. **65**: 453–471. 1942.
40. Fidler, J. C. Studies in zymasis. VII. The estimation of the ethyl alcohol and acetaldehyde content of apples. Biochem. Jour. **28**: 1107–1120. 1934.
41. ————. The function of acetaldehyde in the catabolism of carbohydrate. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1935: 115. 1936.

42. Fisher, D. V. Storage of Delicious applies in artificial atmospheres. Am. Soc. Hort. Sci., Proc. **37**: 459–462. 1939.
43. ———— and Britton, J. E. Maturity and storage studies with peaches. Sci. Agr. **21**: 1–17. 1940.
44. Fontanel, L. Activating effects of ripened fruits on neighboring fruit. Proc. 7th Int. Cong. Refrig. Hague **4**: 79–80. 1936.
45. Gane, R. Volatile products of the metabolism of apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1931: 241–242. 1932.
46. ————. Production of ethylene by ripening fruits. Nature **134**: 11008. 1934.
47. ————. The identification of ethylene among the volatile products of ripe apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1934: 122–123. 1935.
48. ————. Volatile products of fruits. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1935: 127. 1936.
49. ————. The formation of ethylene by plant tissues and its significance in the ripening of fruit. Jour. Pom. & Hort. Sci. **13**: 351. 1935.
50. ————. The production of a physiologically active vapor by unripe pears. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1938: 142–43. 1939.
51. Gerhardt, F. Simultaneous measurement of carbon dioxide and organic volatiles in the internal atmosphere of fruits and vegetables. Jour. Agr. Res. **64**: 207–219. 1942.
52. ———— and Ezell, B. D. Effect of carbon dioxide storage on Bartlett pears under simulated transit conditions. Jour. Agr. Res. **56**: 121–136. 1938.
53. ———— and ————. A method of estimating the volatile products liberated from stored fruit. Jour. Agr. Res. **58**: 493–503. 1939.
54. ———— and ————. Physiological investigations on fall and winter pears in the Pacific Northwest. U. S. Dept. Agr., Tech. Bul. 759. 1941.
55. ———— *et al.* Respiration, internal atmosphere, and moisture studies of sweet cherries during storage. Am. Soc. Hort. Sci., Proc. **41**: 119. 1942.
56. ———— and Ryall, A. L. Storage of sweet cherries as influenced by carbon dioxide and volatile fungicides. U. S. Dept. Agr., Tech. Bul. 631. 1939.
57. ———— *et al.* Effect of carbon dioxide on apricots and peaches under simulated transit. Am. Soc. Hort. Sci., Proc. **38**: 243–248. 1941.
58. Gore, H. C. Studies on fruit respiration. U. S. Dept. Agr., Chem. Bul. 142. 1911.
59. Gourley, J. H. and Hopkins, E. F. Nitrate fertilization and keeping quality of fruit. Ohio Agr. Exp. Sta., Bul. 479. 1931.
60. Green, W. P. *et al.* Calorimetric measurements of the heat of respiration of fruits and vegetables. U. S. Dept. Agr., Tech. Bul. 771. 1941.
61. Griffiths, E. and Awberry, J. H. Heat generated by fruit. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1927: 88. 1928.
62. Haines, D. The acid content of stored apples and its significance. Ann. Bot. **39**: 77. 1925.
63. Haller, M. H. Changes in the pectic constituents of apples in relation to softening. Jour. Agr. Res. **39**: 739–746. 1929.
64. ———— and Harding, P. L. Effects of storage temperature on peaches. U. S. Dept. Agr., Tech. Bul. 680. 1939.
65. ———— and Lutz, J. M. Soft scald of Jonathan apples in relation to respiration. Am. Soc. Hort. Sci., Proc. **34**: 173–176. 1937.

66. ———— AND ————. A comparative study of storage at 32° F. and 36° F. of apples grown in the Potomac River Valley. U. S. Dept. Agr., Tech. Bul. 776: 1–41. 1941.
67. ———— *et al.* The respiration of some fruits in relation to temperature. Am. Soc. Hort. Sci., Proc. **28**: 583–589. 1932.
68. HANES, C. S. AND MORRIS, T. N. Transformation of pectic constituents of plums during normal and abnormal ripening. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1938: 129–132. 1939.
69. HANSEN, E. Quantitative study of ethylene production in relation to respiration of pears. Bot. Gaz. **103**: 543–559. 1942.
70. ———— AND HARTMAN, H. The occurrence in pears of metabolic gases other than carbon dioxide. Or. Agr. Exp. Sta., Bul. 342. 1935.
71. ———— AND ————. Effect of ethylene and certain metabolic gases upon respiration and ripening of pears before and after cold storage. Pl. Physiol. **12**: 441. 1937.
72. ———— AND ————. Chemical determination of ethylene in the emanations from apple and pears. Bot. Gaz. **101**: 403–409. 1939.
73. HARDING, P. L. Distribution of total soluble solids and catalase in different parts of Jonathan apples. Jour. Agr. Res. **53**: 43–48. 1936.
74. ————. Respiration of Grimes Golden apples under various controlled temperatures. Am. Soc. Hort. Sci., Proc. **26**: 319–324. 1929.
75. ————. Physiological behavior of Grimes Golden apples in storage. Ia. Agr. Exp. Sta., Res. Bul. 182. 1935.
76. HARLEY, C. P. AND FISHER, D. B. The occurrence of acetaldehyde in Bartlett pears and its relation to pear scald and breakdown. Jour. Agr. Res. **35**: 983–993. 1927.
77. HARVEY, E. M. The ripening of fruits by ethylene gas. Minn. Hort. **54**: 140. 1926.
78. HAYNES, D. AND ARCHBOLD, H. K. Chemical studies in the physiology of the apple. Ann. Bot. **42**: 965–1017. 1928.
79. HEULIN, F. E. *et al.* The cool storage of peaches: in air and artificial atmospheres. Jour. Dept. Agr. Vict. **35**: 609–614. 1937.
80. HIBBARD, R. P. The physiological effect of ethylene gas upon celery, tomatoes and certain fruits. Mich. Agr. Exp. Sta., Tech. Bul. 104. 1930.
81. HILL, G. R. Respiration of fruits and growing plant tissues in certain gases with reference to ventilation and fruit storage. Cornell Agr. Exp. Sta., Bul. 330. 1913.
82. HINTON, J. C. Studies on maturity of fruit. VI. The effect of conditions during growth on some chemical constituents of apples in storage. Long Ashton Res. Sta., Ann. Rep. 1934: 84. 1935.
83. HOFBAUER, GEORG. Die Warmenatmung reifender Fruchte. (Wien.) Staatl. Tech. Versuchsamt. Mitt. **16**: 119–123. 1927.
84. HOPKINS, E. F. AND GOURLEY, J. H. A study of the ash constituents of apple fruits during the growing season. Ohio Agr. Exp. Sta., Bul. 519. 1933.
85. HULME, A. C. The acetaldehyde and ethyl alcohol contents of apples during storage. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1933: 70–71. 1934.
86. ————. The metabolism of nitrogen in apple fruits. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1935: 126–131. 1936.
87. ————. A tree injection experiment on the keeping quality of apples. East Malling Res. Sta., Ann. Rep. 1936: 185. 1937.
88. ———— AND SMITH, W. H. A relationship between protein content and rate of respiration in the cell of the apple. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1938: 127–128. 1939.

89. Isaac, W. E. The evolution of a growth inhibiting emanation from peaches and plums. Roy. Soc. So. Africa, Trans. 26: 307. 1938.
90. ———. Investigations of the active substance produced by peaches and plums. So. Africa Dept. Agr., Low Temp. Res. Sta., Bul. 1937–38: p. 93. 1939.
91. ———. The effect of ripe Peregrine peaches on the respiration of unripe fruit of the same variety at 90° F. So. Africa Dept. Agr., Low Temp. Res. Sta., Rep. 1938–39: 71. 1940.
92. Kidd, F. Influence of fungal invasion and mechanical injury upon the rate of carbon dioxide production of apples. So. Africa Dept. Agr., Low Temp. Res. Sta., Rep. 1931: 111–114. 1932.
93. ——— and Hanes, C. S. Hydrogen ion concentration in apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1936: 133. 1937.
94. Kidd, F. and West, C. A relation between the respiratory activity and keeping quality of apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1925: 37–41. 1926.
95. ——— and ———. A relation between the concentration of oxygen and carbon dioxide in the atmosphere on rate of respiration and length of storage life in apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1925: 41–45. 1927.
96. ——— and ———. Forecasting the life of an apple. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1927: 23–27. 1928.
97. ——— and ———. Respiration of pears in air and other mixtures of oxygen and nitrogen at 1° C. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1928: 36. 1929.
98. ——— and ———. Physiology of fruit. I. Changes in the respiratory activity of apples during their senescence at different temperatures. Royal Soc., Proc. B. 106: 93–109. 1930.
99. ——— and ———. Effects of ethylene and apple vapors on the ripening of fruits. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1932: 55–58. 1933.
100. ———. The respiration of fruits. Paper read before the Royal Inst. of Great Britain, Nov. 9, 1934.
101. ——— and ———. The cause of low temperature breakdown in apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1933: 57–60. 1934.
102. ——— and ———. The influence of the composition of the atmosphere upon the incidence of the climacteric in apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1933: 51–57. 1934.
103. ——— and ———. The effects of ethyl alcohol upon the respiratory metabolism of apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1933: 60–67. 1934.
104. ——— and ———. The internal atmosphere of apples in gas storage. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1934: 110. 1935.
105. ——— and ———. The effect of ethylene on apples at low temperature: evidence for the production of ethylene by unripe, immature fruit. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1934: 119–122. 1935.
106. ——— and ———. Temperature and duration of life of apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1935: 97–102. 1936.
107. ——— and ———. Gas storage of English grown Conference pears. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1935: 102–110. 1936.
108. ——— and ———. The keeping qualities of apples in relation to their maturity when gathered. Sci. Hort. 5: 78. 1937.

109. ———— AND ————. The action of carbon dioxide on the respiratory activity of apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1937: 101. 1938.
110. ———— AND ————. The effect of ethylene on the respiratory activity and the climacteric of apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1937: 108. 1938.
111. ———— AND ————. The uptake of oxygen by apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1937: 102–108. 1938.
112. ———— AND ————. Individual variation in apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv Bd., Rep. 1937: 114. 1938.
113. ———— AND ————. Spotting and other effects on apples in storage due to volatile products from ripe apples of other varieties stored with them. Jour. Pom. & Hort. Sci. **16**: 274–279. 1938.
114. ———— *et al.* Rise in insoluble fraction of total nitrogen during climacteric in apples and pears and effect of the phenomenon on retarding the climacteric by carbon dioxide or stimulating the climacteric by ethylene. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1938: 119–125. 1939.
115. ———— *et al.* Sorbitol in pears and its conversion during storage into fructose units. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1938: 132–126. 1939.
116. ———— AND ————. The production of volatiles by apples: effects of temperature, maturity, technique of estimation, etc. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1938: 136–139. 1939.
117. ———— AND ————. The rate of respiration and production of volatiles of Conference pears: effects of treatment with ethylene, temperature and wounding. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1938: 139–142. 1939.
118. KOSTYCHEV, S. Plant respiration. 1927.
119. KROTOV, G. The respiration metabolism of McIntosh apples during ontogeny as determined at 22° C. Pl. Physiol. **16**: 799–812. 1941.
120. LUTHRA, J. C. Some experiments on the effects of dry and moist air on the rate of respiration and breakdown of ripe pears. New Phytol. **23**: 131–142. 1924.
121. LUTZ, J. M. AND CULPEPPER, C. W. Certain chemical and physical changes produced in Kieffer pears during ripening and storage. U. S. Dept. Agr., Tech. Bul. 590. 1937.
122. LYNCH, L. J. A suggested co-enzyme hypothesis for the ripening of fruits by ethylene gas treatment. Roy. Soc. Queens, Proc. **47**: 18. 1936.
123. MAGNESS, J. R. AND BALLARD, W. S. The respiration of Bartlett pears. Jour. Agr. Res. **32**: 801–832. 1926.
124. ———— AND BURROUGHS, A. M. Storage investigations. Marble Lab. Inc., Rep. **2**: 17–98. 1923.
125. ———— AND DIEHL, H. C. Physiological studies on apples in storage. Jour. Agr. Res. **27**: 1–38. 1924.
126. ———— *et al.* Ripening, storage and handling of apples. U. S. Dept. Agr., Bul. 1406. 1926.
127. MARKLEY, K. S. *et al.* Further studies on the wax-like coating of apples. Jour. Biol. Chem. **98**: 103–107. 1932.
128. ———— *et al.* Constituents of the wax-like coating of the pear. Pyrus communis. Jour. Biol. Chem. **111**: 133–146. 1935.
129. ———— AND SANDO, C. E. Progressive changes in the wax-like coating on the surface of the apple during growth and storage. Jour. Agr. Res. **42**: 705–722. 1931.
130. ———— AND ————. Progressive changes in the cuticle of apples during growth and storage. Jour. Agr. Res. **46**: 403–412. 1933.

131. Marshall, R. E. *et al.* The relation of washing treatment to subsequent losses in moisture from apples. Wash. Agr. Exp. Sta., Bul. 330: 1–28. 1936.
132. Martin, W. E. The distribution of certain sugars in Bosc pears. Pl. Physiol. 11: 139–147. 1936.
133. ————. Chemical study of the ripening process of Bosc pears. Bot. Gaz. 99: 42–68. 1937.
134. Matsumoto, K. Studies on the physiological changes in peaches during handling and railroad shipment. Kyoto Univ. Col. Agr., Mem. 46: 79. 1939.
135. Miller, E. V. Distribution of acetaldehyde and alcohol in the apple fruit. Jour. Agr. Res. 53: 49–55. 1936.
136. ———— and Brooks, C. Effect of carbon dioxide content of storage atmosphere on carbohydrate transformation in certain fruits and vegetables. Jour. Agr. Res. 45: 449–459. 1932.
137. ———— and Dowd, O. J. Effect of carbon dioxide on the carbohydrates and acidity of fruits and vegetables in storage. Jour. Agr. Res. 53: 1–17. 1936.
138. Morse, F. W. The respiration of apples and its relation to their keeping. N. H. Agr. Exp. Sta., Bul. 135. 1908.
139. Nelson, E. K. The non-volatile acids of the peach. Am. Chem. Soc., Jour. 46: 2337–2338. 1924.
140. Nelson, R. C. The quantity of ethylene present in apples. Pl. Physiol. 12: 1004–1005. 1937.
141. ————. Studies on production of ethylene in the ripening processes in apples and banana. Food Res. 4: 173–190. 1939.
142. ————. Quantitative study of the production of ethylene by ripening McIntosh apples. Pl. Physiol. 15: 149–151. 1940.
143. Onslow, M. *et al.* Biochemical study of senescence in apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1928: 31. 1929.
144. ———— *et al.* Biochemical study of senescence in apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1929: 44–52. 1930.
145. ———— *et al.* Biochemical study of senescence. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1931: 52–77. 1932.
146. Perry, W. and Martin, J. M. The cutinization of apple skins in relation to their keeping qualities and their environment. Iowa State Hort. Soc., Rep. 52: 180–192. 1917.
147. Phillips, W. R. Application of controlled atmospheres in storage of fruits. Sci. Agr. 19: 66–68. 1938.
148. ————. Respiration curves for McIntosh apples. Sci. Agr. 19: 505. 1939.
149. Pieniazek, S. A study of factors influencing the rate of transpiration of apple fruits. Cornell Univ., Ph.D. thesis 1942.
150. ————. Maturity of apple fruits in relation to the rate of transpiration. Am. Soc. Hort. Sci., Proc. 42: 231–237. 1943.
151. Plagge, H. H. Controlled atmosphere storage for Jonathan apples. Refrig. Eng. 43: 215–220. 1942.
152. ———— and Gerhardt, F. Acidity changes associated with the keeping quality of apples under various storage conditions. Iowa Agr. Exp. Sta., Res. Bul. 131. 1930.
153. ———— *et al.* Certain physical and chemical changes of Grimes apples during ripening and storage period. Iowa Agr. Exp. Sta., Res. Bul. 91: 43–71. 1926.
154. Power, F. B. and Chestnut, V. K. The odorous constituents of apples. Emanation of acetaldehyde from the ripe fruit. Am. Chem. Soc., Jour. 42: 1509. 1920.
155. ———— and ————. The odorous constituents of peaches. Am. Chem. Soc., Jour. 43: 1725. 1921.

156. ———— AND ————. The odorous constituents of apples. II. Evidence of the presence of geraniol. Am. Chem. Soc., Jour. **44**: 2938–2942. 1922.
157. ROBERTS, E. H. Chemistry of plant respiration. Current Sci. **9**: 272–273. 1940.
158. ROSE, D. H. *et al.* The commercial storage of fruits, vegetables and florists stocks. U. S. Dept. Agr., Cir. 278. 1941.
159. ROUX, E. R. Respiration and maturity in peaches and plums. Ann. Bot. **4**: 317–327. 1940.
160. RYALL, A. L. Certain physiological effects of carbon dioxide treatments of plums. Am. Soc. Hort. Sci., Proc. **32**: 164. 1935.
161. ———— AND ALDRICH, W. W. The effects of water deficits in the tree upon maturity, composition and storage quality of Bosc pears. Jour. Agr. Res. **68**: 121–133. 1944.
162. SHAW, S. T. Respiration studies of developing Jonathan apples. Pl. Physiol. **17**: 80–91. 1942.
163. SMITH, A. J. M. The generation of heat by respiring fruit. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1928: 53. 1929.
164. ————. Evaporation from apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1931: 152–153. 1932.
165. ————. Evaporation from foodstuffs. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1932: 117–138. 1933.
166. ————. Equilibria between water and water vapor. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1933: 105–111. 1934.
167. ————. Evaporation from plums. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1933: 105–111. 1934.
168. SMITH, W. H. Loss of water from apples in relation to relative humidity. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1929: 54–56. 1930.
169. ————. Loss of water from fruit. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1930: 55–61. 1931.
170. ————. Internal factors determining rate of loss of water from fruit. Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1931: 106–107. 1932.
171. ————. Evaporation of water from apples in relation to temperature and atmospheric humidity. Ann. Appl. Biol. **20**: 220–235. 1933.
172. SMOCK, R. M. Certain effects of wax treatments on various varieties of apples and pears. Am. Soc. Hort. Sci., Proc. **33**: 284–289. 1936.
173. ————. Some additional effects of waxing apples. Am. Soc. Hort. Sci., Proc. **37**: 448–452. 1940.
174. ————. Influence of controlled atmosphere storage on the respiration of McIntosh apples. Bot. Gaz. **104**: 178–184. 1942.
175. ————. The influence of one lot of apples on another. Am. Soc. Hort. Sci., Proc. **40**: 187–192. 1942.
176. ————. The influence of stored apples on the ripening of other apples stored with them. Cornell Agr. Exp. Sta., Bul. 799. 1943.
177. ———— AND ALLEN, F. W. Soluble pectin changes in gas stored fruit. Am. Soc. Hort. Sci., Proc. **35**: 184. 1937.
178. ———— AND VAN DOREN, A. Controlled atmosphere storage of apples. Cornell Agr. Exp. Sta., Bul. 762. 1941.
179. SOUTHWICK, F. W. The volatile production of apples and its relation to the apple scald disease. Cornell Univ., Ph.D. thesis 1943.
180. STILES, WALTER AND LEACH, WILLIAM. Respiration in plants. 1932.
181. TAYLOR, R. H. AND OVERHOLSER, E. L. Some effects of high temperature and humidity on the keeping quality of Bartlett pears. Cal. Comm. Hort., Month. Bul. **8**: 118–125. 1919.

182. Thomas, M. The controlling influence of carbon dioxide. V. A quantitative study of the production of ethyl alcohol and acetaldehyde by cells of the higher plants in relation to concentration of oxygen and carbon dioxide. Biochem. Jour. **19**: 927. 1925.
183. ————. Biochemical investigations on the storage diseases of apples, with special reference to aldehyde poisoning. First Imp. Hort. Conf., Proc. Part III: 98–101. 1931.
184. Thompson, F. and Whittier, A. C. Forms of sugar found in common fruits. Am. Soc. Hort. Sci., Proc. **9**: 16–22. 1913.
185. Thornton, N. C. Carbon dioxide storage. III. The influence of carbon dioxide on the oxygen uptake by fruits and vegetables. Boyce Thomp. Inst., Contr. **5**: 371–402. 1933.
186. ————. Carbon dioxide storage. IV. The influence of carbon dioxide storage on the acidity of plant tissue. Boyce Thomp. Inst., Contr. **5**: 403–418. 1933.
187. Tindale, G. N. *et al.* Victoria plums and peaches: cool storage and export. Dept. Agr., Victoria, Jour. 1939: 1–12. 1940.
188. Trout, S. A. Effect of volatile products on the storage life of fruit. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1929: 60. 1930.
189. ———— *et al.* Studies in the metabolism of the apple. I. Preliminary investigations on internal gas composition and its relation to changes in stored Granny Smith apples. Australian Jour. Exp. Biol. & Med. Sci. **20**: 219–231. 1942.
190. ———— and Kidd, F. The role of acetaldehyde in the respiration of plants. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1931: 78. 1932.
191. Van Der Plant, J. E. and Van Wyk, G. F. Delayed storage and treatment with acetylene gas as aids to the ripening of Bon Chretein pears at 45° F. So. Africa Dept. Agr., Low Temp. Res. Sta., Rep. 1938–39. 9. 1940.
192. Van Doren, A. Physiological studies with McIntosh apples in modified atmosphere cold storage. Am. Soc. Hort. Sci., Proc. **37**: 453–458. 1939.
193. ————. The influence of controlled atmospheres on the storage life and keeping qualities of certain varieties of apple fruits. Cornell Univ., Ph.D. thesis. 1941.
194. ———— *et al.* Carbon dioxide treatment of strawberries and cherries in transit and storage. Am. Soc. Hort. Sci., Proc. **38**: 231–238. 1941.
195. Wallace, T. Factors influencing the storage qualities of fruits. First Imp. Hort. Conf., Proc. Part III: 9–24. 1931.
196. Walls, L. P. The nature of the volatile products from apples. Pom & Hort. Sci., Jour. **20**: 59–67. 1942.
197. West, C. Effect of climatic conditions upon the storage life of apples. [Gr. Br.] Dept. Sci. & Ind. Res., Food Inv. Bd., Rep. 1929: 52–54. 1930.
198. Watson, Ross. Ozone as a fungicide. Cornell Univ., Ph.D. thesis. 1942.

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| **Plant Disease Introduction** | W. A. MCCUBBIN<br>*Bureau of Entomology and Plant Quarantine* |
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| **Modern Views and Facts About Growth Substances** | P. W. ZIMMERMAN<br>*Boyce Thompson Institute for Plant Research* |

## Proposed Future Contents of
# THE BOTANICAL REVIEW

### *Articles received and awaiting publication*

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| **Antibiotic Substances Derived from Micro-organisms** | J. C. HOOGERHEIDE<br>*Corsan Research Laboratories* |
| **Plant Fats in Relation to Environment and Evolution** | JAMES B. MCNAIR |

### *Articles arranged for most recently*

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| **Mineral Nutrition of Plants as Affecting Mineral Nutrition of Animals, Including Man** | L. A. MAYNARD and K. BEESON<br>*Cornell University* |
| **Rubber Formation in Plants** | JAMES BONNER and D. A. GOLDSTON<br>*California Institute of Technology* |

### *Articles in course of preparation*

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| **The Cytology of Fertilization in Angiosperms** | L. E. ANDERSON<br>*Duke University* |
| **Development of the Madro-Tertiary Flora** | D. I. AXELROD<br>*University of California* |
| **Relation of Wood Anatomy to Taxonomy** | I. W. BAILEY<br>*Harvard University* |
| **Anthocyanin Pigments** | F. BLANK<br>*Switzerland* |
| **The Genetics of Pollen Tube Growth** | J. T. BUCHHOLZ<br>*University of Illinois* |
| **Sexuality and Genetics of Algae** | H. BOLD and W. G. WHALEY<br>*Columbia University* |
| **Role of the Endosperm in Seed Development** | R. A. BRINK and D. C. COOPER<br>*University of Wisconsin* |
| **Heart Rots in Living Trees** | R. W. DAVIDSON<br>*Bureau of Plant Industry* |
| **The Angiosperm Embryo Sac** | EMMA L. FISK<br>*University of Wisconsin* |
| **Cytogenetics of Nicotiana** | T. H. GOODSPEED<br>*University of California* |
| **American Agar Industry** | H. J. HUMM<br>*Duke Marine Laboratory* |
| **Laboratory Testing of Spraying and Dusting Fungicides** | J. G. HORSFALL<br>*Connecticut Agriculture Experiment Station* |
| **Destructive Foreign Plant Diseases not known to be established in North America** | N. REX HUNT<br>*Bureau of Entomology and Plant Quarantine* |
| **Cytology and Genetics in Relation to Taxonomy** | C. L. HUSKINS<br>*McGill University* |
| **A Critical Survey of the Present Status of Plant Embryology** | D. A. JOHANSEN<br>*Stanford University, Cal.* |
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| **Endomitosis** | A. LORZ<br>*Seton Hall College* |
| **Tropical Fruits and Their Future** | S. J. LYNCH<br>*Sub-tropical Experiment Station* |
| **Paleobotanical Taxonomy** | H. L. MASON<br>*University of California* |

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